THE UNIVERSITY OF ALBERTA

AUTECOLOGICAL STUDIES OF *LUZULA CONFUSA*: A PLANT'S RESPONSE TO THE HIGH ARCTIC ENVIRONMENT ON KING CHRISTIAN ISLAND, N.W.T.

by

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Autecological Studies of *Luzula confusa*: A Plant's Response to the High Arctic Environment on King Christian Island, N.W.T." submitted by Paul Addison in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Plant Ecology.

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ABSTRACT

At Cape Abernathy on King Christian Island ($77^{o}45'N$, $101^{o}10'W$), the question of what adaptations were advantageous in survival and growth of Luzula confusa in the high arctic environment was examined.

Much of King Christian Island is Polar Desert (<2% vascular plant cover) with Polar Semi-desert (2-20% vascular plant cover) occupying a band 1.5 Km wide about 1 Km from the coast. The island is highly dissected owing to water erosion and, plant communities in the Polar Semi-desert appear to be delimited by snow whose cover is dictated by the terrain. The maritime summer climate (July and August averages from 1973-1975) is characterized by low temperature ($2.5^{o}C$), low precipitation (43 mm), moderate wind speed ($3.3\ m\ sec^{-1}$), high relative humidity (90%) and a high incidence of cloud and fog (80%). Microenvironments are dominated by the thermal regime. Since air holds little water vapour at low temperatures, and surface to air temperature gradient was shallow, evapotranspiration was low. Cloud cover however, was high and this completed the cycle by reducing the amount of global radiation received and keeping both the thermal gradient (surface to atmosphere) and air temperature low. Net radiation was 68% of global radiation ($.207\ cal\ cm^{-2}\ min^{-1}$) and was mainly dissipated by sensible heat flux (62%). Both latent heat flux (27%) and soil heat flux (11%) were small components of net radiation. Resistances to heat and water loss were low

($< .5$ sec cm^{-1}) owing to the smooth surface (z_o = .01-.05 cm) and moderate wind speed.

Luzula confusa is a long-lived (110 years) graminoid that appears well adapted to the hostile environment on King Christian Island. Its tufted growth form with a substantial amount of standing dead material, lends protection to the living tissue throughout the year as well as placing the plant in a warm, near-surface thermal environment. Over 90% of the plant's biomass is within 5 cm of the soil surface. A moss layer also aids in protection of living tissue and appears to provide the necessary seedbed for plant establishment. Reproduction of L. confusa is mainly asexual through the production of tillers from an underground rhizome.

L. confusa cannot withstand drought and its photosynthetic rate drops dramatically with decreasing water potential. The response of the plant to light and temperature however, is similar to that of other arctic graminoids and net photosynthesis can be positive throughout the 24 hr arctic day. The potential for net photosynthesis is much higher in the spring than in summer owing to higher temperature and light. Low summer temperature appears to be the most important factor in controlling plant metabolism.

In general, Luzula confusa appears to be both morphologically and physiologically adapted to the Polar Semi-

desert environment on King Christian Island. This species combines the more efficient graminoid photosynthetic system with some of the cushion plant energy trapping characteristics. In this way, the plant is able to assimilate carbon positively and rapidly at low temperatures. In addition, the plant takes advantage of the optimal growing conditions that occur immediately after snow-melt.

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INTRODUCTION

In arctic regions, the abiotic environment appears to be much more important than biotic interactions in the survival, growth and reproduction of plants (Billings 1974). This is especially true in Polar Desert and Polar Semi-desert areas where scattered plants are exposed to some of the most rigorous environments on earth. In these areas, climate is thought to be the dominant driving force that causes particular plant morphological and physiological characteristics, usually defined as plant adaptations.

Since the direct response of the plant is to its microenvironment, analysis of microclimate is essential in studies of plant-environment interactions. This climate near the ground however, is largely a function of energy exchange phenomena at the ground-air interface (Bliss et al. 1973). In this study, energy budgets as well as mass and momentum transfer considerations were used to establish why certain microenvironments occurred where and when they did.

Luzula confusa is one of the most common and widespread of all arctic plants (Polunin 1948) and, as such, is exposed to a great variety of microenvironments. Since this species is so successful, it was expected that it would show morphological and physiological characteristics that may be considered as "ideally suited" for arctic

survival and growth. The increased activity of petroleum exploration and development in the far north in recent years has made quantification of plant characteristics very important. It was hoped that a plant species that naturally occurred in a wide variety of habitats might also have sufficient ecological plasticity to survive in man-modified microenvironments. Selection of plant species for revegetation of perturbated areas becomes much less difficult if plant adaptations to both arctic and disturbed environments are known.

The question "What plant adaptations are necessary for survival and growth in the high arctic environment?" can only be answered through a combined study of environment and plant response. This type of study entails description of both the plant and its environment in the field, and measurement of plant response in the field and under controlled conditions. In the past, very few such studies were carried out on native plant species and, in the Arctic, only the International Biological Program (I.B.P.) had sufficient support, expertise and coordination to bring together meteorology and plant physiology in order to quantify plant adaptations to specific environments. In the arctic I.B.P. studies, the advantages of both cushion growth form and upright stance in their respective environments were quantified using energy relations and water and carbon balance studies. Luzula confusa is a tufted graminoid and represents a third growth form found commonly

in arctic areas. It was expected that this plant might be adapted to the moist Polar Semi-desert conditions predominating the northwest Queen Elizabeth Islands. This study was designed to compliment the I.B.P. and examine adaptations of L. confusa from a micrometeorological-plant physiological viewpoint.

The aims of this study were: 1) to characterize selected physical environments on King Christian Island; 2) to examine the dynamics of microenvironment through energy and mass transfer considerations; 3) to describe several morphological and physiological characteristics of Luzula confusa, and 4) to determine adaptations of Luzula that permits the species to survive and grow in this rigorous environment.

DESCRIPTION OF SITE

King Christian Island is located in the north-central part of the Queen Elizabeth Islands approximately 40 Km south of Ellef Ringnes Island (Fig 1). The island is small (ca. 1000 Km^2) and has little relief with most areas below 150 m AMSL. Little geological work other than that associated with petroleum exploration has been done on the island although the larger islands to the north have been studied (Ellef Ringnes and Amund Ringnes; Heywood 1957, Fortier et al. 1963). Geologically, the island is a typical part of the lowland of central and southern Ellef Ringnes Island and is underlain by shale with minor limestone and weakly indurated sandstone (Roots in Fortier et al. 1963). The surface is covered by alluvial and deltaic sands and marine beach deposits (Greiner in Fortier et al. 1963, Pawluk and Brewer 1975).

Much of the topography has originated from water erosion (Plate 1) as on other islands of the Sverdrup group (St. Onge 1964). Low ridges are also in evidence (Plate 2) and result from complex folding during Tertiary time (Roots in Fortier et al. 1963). In general, the coastal part of King Christian Island is a lowland that has numerous small valleys (2-3 m deep) cut by seasonal streams.

The summer climate of the island is maritime in nature and has low diurnal fluctuations of temperature and a high

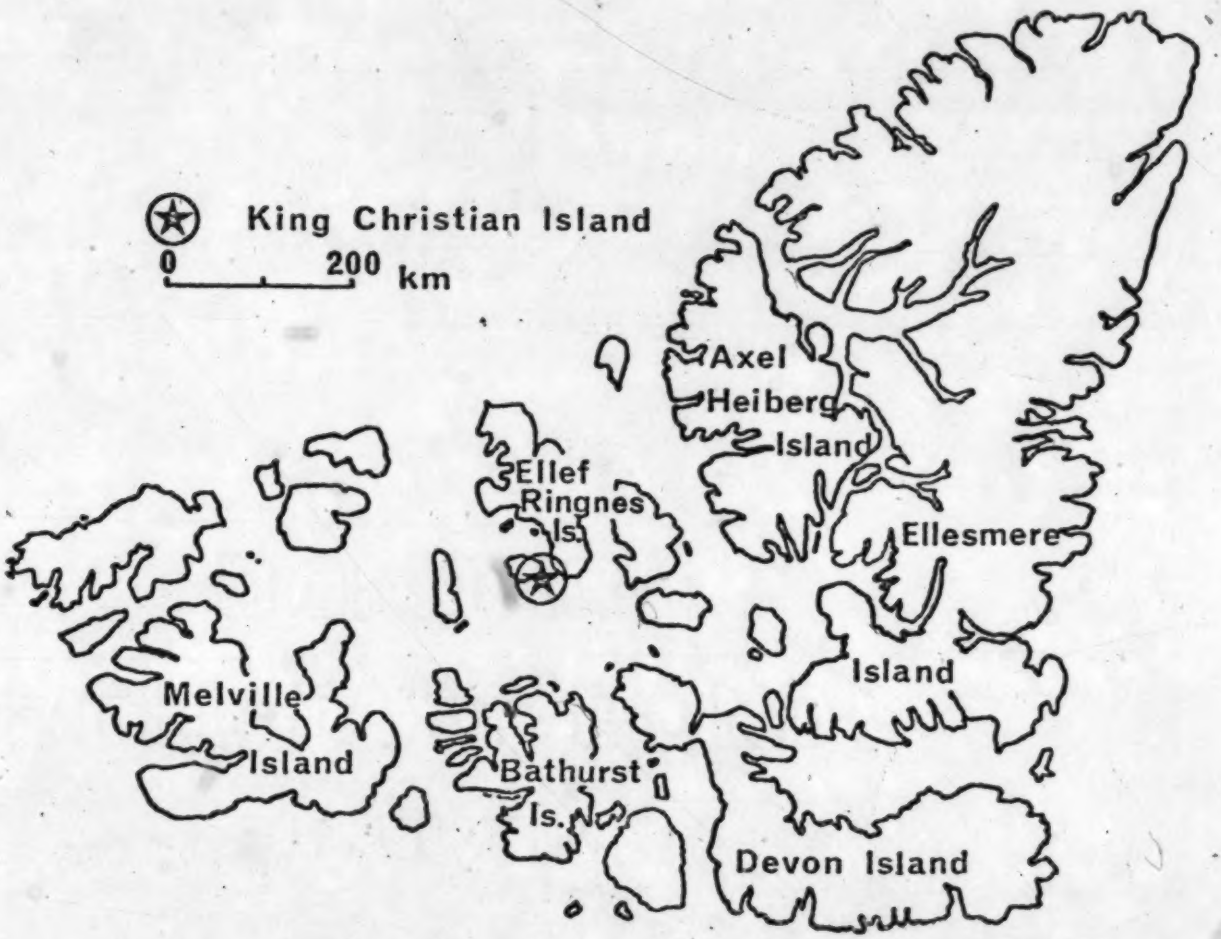

Figure 1. Queen Elizabeth Islands showing the position of King Christian Island Study Site.

Plate 1. Landform result of severe water erosion in the lowland areas of King Christian Island.

Plate 2. Rock outcrops in low ridges in the central part of King Christian Island as a result of folding.

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frequency of fog and light rain. Sea ice cover did not appear to play a dominant role in controlling climatic conditions as seems to be the case at other arctic sites (Tanquary Fiord, Ellesmere Island, Barry and Jackson 1969; Truelove Inlet, Devon Island, Courtin and Labine 1976). The summer (July and August) climate of the area is characterized by cool temperature, low precipitation, moderate wind speed, high relative humidity, and a high incidence of cloud and fog (Thompson 1967, Barry and Hare 1974). A more detailed treatment of climate is presented in Climatology and Microclimatology (p 17).

Vegetative cover varies from 0 - 15% (vascular plants) and the island is mainly Polar Desert with a few Polar Semi-desert areas (sensu Bliss et al. 1973). The greatest plant cover in the northeast part of the island appears to be localized in a band between 1 and 2.5 Km from the coast and the rest of the area is essentially barren (< 1% vascular plant cover). There are however, a few isolated pockets of vegetation dominated by bryophytes in drainage ways. In the Polar Semi-desert area, snow cover appears to delimit plant communities on a gross scale whereas small scale vegetational pattern appears to result from soil moisture differences. A detailed discussion of some of the more extensive plant communities in the northeastern part of the island is presented under Plant Communities (p 10).

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There was little evidence of soil development under any of the plant communities examined and all soils of the area are classified as Regosolic Static Cryosols (Canadian Soil Survey Committee 1973) or Pergellic Cryaquents (Soil Survey Staff (U.S.) 1967). Pawluk and Brewer (1975) indicate that what little soil development there was on King Christian Island may be more closely related to weak "solonetzic" rather than weak "podzolic" processes as suggested by Tedrow (1968) for other Polar Desert soils. This difference was attributed to the very low Ca^{++}/Na^{+} ratios (< 3) of the parent material originating from marine deposits.

A site was selected on the northeast end of the island (Cape Abernathy; 77° 45' N, 101° 10' W) near the Sun Oil Company exploration base camp. An intensive site was chosen in each of a Lichen-Moss-Rush and a Moss-Lichen-Rush community (Plant Communities p 10). These two communities predominate in the Polar Semi-Desert area of the island. Both communities had similar species composition but the differences in moss cover and bare soil were sufficiently great to consider each as a separate entity.

The surface of the Lichen-Moss-Rush community was subdivided into six microsites for energy and water relations purposes (Table 1); lichens, bare soil, moss, and three vascular plants, Luzula confusa[1], Potentilla hyparctica and Saxifraga caespitosa that were considered representative of the three

1. Nomenclature for vascular species follows Porsild (1964)

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major plant growth forms. Luzula confusa represented the upright graminoids such as Alopecurus alpinus, Luzula nivalis and Festuca brachyphylla whereas Potentilla hyparctica represented broadleaved species like Papaver radicatum, Ranunculus sabinei, Saxifrage nivalis and S. cernua, and Saxifraga caespitosa represented the cushion growth form that includes Draba spp. and Cerastium alpinum.

The heterogeneous surface of the Moss-Lichen-Rush community also necessitated subdivision for energy budget work, and the same microsites as at the Lichen-Moss-Rush community were selected. Owing to the absence of Saxifraga caespitosa at this site, the few cushion plants were included with the broadleaved species (Table 1).

Table 1. Characteristic species and percent cover of 6 microsites from Lichen-Moss-Rush and Moss-Lichen-Rush communities on King Christian Island.

Microsite	Characteristic Species	Percent Cover	
		Lichen-Moss -Rush	Moss-Lichen -Rush
Lichen	Black terricolous crust	40.1	42.3
Moss	Rhacomitrium lanuginosum Oncophorus wahlenbergia	18.0	44.9
Unvegetated		33.2	1.4
Upright Graminoids	Luzula confusa	3.5	6.8
Broadleaved	Potentilla hyparctica	3.4	4.6
Cushions	Saxifraga caespitosa	1.8	*

* Cushion Plants (1.2%) have been included in the Broadleaved Microsite.

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PLANT COMMUNITIES

INTRODUCTION

Many of the plant communities of the Cape Abernathy region of King Christian Island have been described by Bell (1975) and Blundon (1976). This study made no attempt to repeat this work but it was deemed necessary to describe the plant communities near the Sun Oil Company exploration camp to 1) permit expansion of microsite energy relations to the plant communities as units, and 2) estimate the importance of the various factors involved in delimiting plant community types in the area.

METHODS AND MATERIALS

Vegetation was sampled using belt transects (25-40 m long) parallel to the slope of the land and sampling was done with a 25 x 25 cm quadrat. This size of quadrat was larger than the minimum sampling area required as defined by Cain and Castro (1959). End points of the transects were selected subjectively and two continuous transects were run at each site. More than 100 quadrats fell within each of the communities described.

RESULTS AND DISCUSSION

The Lichen-Moss-Rush community (Plate 3) was characterized

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Plate 3. Lichen-Moss-Rush community in the Polar Semi-Desert area of King Christian Island.

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by a substantial amount of lichen covered surface and unvegetated soil. Vascular plant cover (8.7%) was dominated by Luzula confusa, Papaver radicatum, Alopecurus alpinus and Draba spp. with numerous species contributing 0.2 to 0.5% cover (Table 2). Moss cover (18%) was dominated by Rhacomitrium lanuginosum (Hedw.), and terricolous crustose and foliose forms dominated the lichen cover (40.1%). Unvegetated soil comprised 33.2% of this community. The Moss-Rush-dry meadow described by Bell (1975) was equivalent to this community but since lichens predominate and since vascular plants had such a low cover value, the name Lichen-Moss-Rush was preferred.

Luzula nivalis, Alopecurus alpinus, Luzula confusa and Stellaria longipes dominated the vasular plant cover (11.4%) at the Moss-Lichen-Rush community (Plate 4);(Table 2). Moss cover (44.9%) was dominated by Oncophorus wahlenbergia (Brid.) and there was little unvegetated soil (1.4%). Crustose and foliose lichen cover (42.3%) was comparable with that of the Lichen-Moss-Rush community. The Moss-Lichen-Rush community was equivalent to the Moss-Rush-moist meadow described by Bell(1975) but since lichens represented a large proportion of the surface cover (42.3%), and since vascular plants were not sufficiently common to use the term "meadow", the name Moss-Lichen-Rush community was adopted.

Vascular plant cover (mainly Stellaria longipes) of the Lichen-Moss mud boil community (Plate 5) was very low (2.9%).

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Plate 4. Moss-Lichen-Rush community in the Polar Semi-Desert area of King Christian Island.

Plate 5. Lichen-Moss mud boil community along river banks on King Christian Island.

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Table 2. Four plant communities of the Polar Semi-desert area of Northeast King Christian Island. Porsild (1964) is used as the authority for taxonomic names.

Species	Percent Cover			
	Lichen Barrens*	Lichen-Moss Mud Boils	Lichen-Moss -Rush	Moss-Lichen - Rush
Gramineae				
Alopecurus alpinus	.4	.1	1.2	1.8
Festuca brachyphylla			.2	+
Phippsia algida		.5	.2	+
Puccinellia vaginata	.3		+	
Juncaceae				
Juncus biglumus				.1
Luzula confusa			1.4	1.7
Luzula nivalis		.1	.4	3.2
Polygonaceae				
Oxyria digyna	.4			
Caryophyllaceae				
Arenaria rubella	.3	+	.2	
Cerastium arcticum	.2		.3	.2
C. regellii				+
Stellaria longipes		1.0	.4	1.2
Ranunculaceae				
Ranunculus sabinei		+	.5	.4
Papaveraceae				
Papaver radicatum		.2	1.4	.3
Cruciferae				
Draba spp.	.4	.2	.8	.9
Cardamine bellidifolia		+	.2	.3
Cochlearia officinalis		+	+	
Saxifragaceae				
Saxifraga cernua		.4	.3	.4
S. caespitosa	.5	+	.2	
S. nivalis		+	.3	.2
S. rivularis		.2	.1	.3
S. flagellaris			.1	
S. foliolosa				.1
S. oppositifolia	.1			
S. tenuis			.1	.2
Rosaceae				
Potentilla hyparctica			.3	.1
Total Vascular Cover	2.6	2.9	8.7	11.4
Moss Cover	.3	29.7	18.0	44.9
Lichen Cover	19.8	46.0	40.1	42.3
Bare Soil	77.3	21.4	33.2	1.4

* From Bell (1975)

\+ <.05% cover

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This community was characterized by lichens (46%) and mosses (29.7%) and 21.4% was unvegetated (Table 2).

As mentioned above (Site Description p 7), these Polar Semi-Desert areas were localized in a band 1.5 Km wide, 1 Km from the coast. In this area, snow cover appears to delimit the plant communities. Lichen barrens (Table 2; Bell 1975) occurred on ridge tops that had a thin snow cover or were blown free in winter. This community is exposed to winter and summer desiccation and abrasion by windborne ice and sand particles. At the other end of the exposure gradient, Lichen-Moss mud boils were confined to areas of deep snow accumulation (>1 m) along stream beds. This community usually had an extremely short growing season that appears to limit vascular plant establishment.

The major factor in the establishment of the Moss-Lichen-Rush community rather than the Lichen-Moss-Rush community appears to be the greater amount of surface water, mainly from snow melt. This latter community had 13.2 cm of snow on June 16, 1974 as compared with 33.9 cm at the Moss-Lichen-Rush community. In addition, snow persisted over the Moss-Lichen-Rush community until the end of July, 1974 and provided a source of water for most of this growing season.

CONCLUSIONS

The plant communities in the Polar Semi-desert areas of northeastern King Christian Island appear to be delimited by

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snow both by its direct influence on protection and growing season length and indirectly through irrigation.

The Lichen-Moss-Rush community had 40.1% lichen cover, 33.2% unvegetated soil, 18% moss cover and 8.7% vascular plant cover. The Moss-Lichen-Rush community on the other hand, had 44.9% moss cover, 42.3% lichen cover, 11.4% vascular plant cover and 1.4% unvegetated soil.

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CLIMATOLOGY AND MICROCLIMATOLOGY

INTRODUCTION

Meteorological measurements in the Arctic are carried out mainly by the Atmospheric Environment Service (AES), Canada Department of Environment (i.e. Boughner and Thomas 1962, Thompson 1967). The Arctic and particularly the high arctic islands, have few places of permanent human settlement and hence, relatively few, widely-separated permanent meteorological stations as compared with more temperate areas. Many researchers, in a variety of disciplines, working in the Arctic, help to fill in the gaps between permanent stations by providing climatological information to AES during the summer months.

The observations carried out in this study were to 1) provide data to the AES network through Polar Continental Shelf Project, Canada Department of Energy Mines and Resources headquarters in Resolute Bay, N.W.T. and 2) provide general climatological information about the site for comparison with other high arctic sites.

Microclimatological studies are a rarity in the Arctic; most being very recent and of only short term (< 3 years). Most studies have been confined to the Low Arctic (for example Wendler 1971, Romanova 1972, Weller and Cubley 1972, Brazel and Outcalt 1973, and Skartveit et al. 1975) with only few carried out in the high arctic islands (Vowinckel 1966, Barry and Jackson 1969, Ohmura 1970, Smith 1975, and Courtin and

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Labine 1976). These studies range in scope from purely a listing of climatological measurements to studies on the influence of micrometeorological parameters on plants and animals.

The aims of the microclimatological component of this study were 1) to describe microenvironments of two plant communities and 2) to provide background environmental information to permit ecological interpretation of plant physiological responses.

METHODS AND MATERIALS

CLIMATOLOGY

Observations were made at 00, 04, 12, 16 and 20 hr G.M.T. and were reported to AES at 00 and 12 hr G.M.T. Methods followed Manobs (Meteorological Division, Canada Department of Environment, 1973) and included maximum, minimum, ambient and dew point temperatures, wind speed and direction, visibility, precipitation, and cloud cover, type and height.

Maximum and minimum temperatures (1.5 m) were measured with a Max-Min Thermometer (Taylor Instrument Co. Model 5458) in an aluminum louvered shelter. Ambient and wet bulb temperatures were measured with a Sling Psychrometer (Taylor Instrument Co.) wetted with distilled water, and dew point temperature was determined from standard psychrometric tables. Wind speed and direction (10 m) were estimated from measurements made at 50 cm and visibility, cloud cover, type and

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height were estimated visually. Precipitation was measured with a Wedge-type Precipitation Gauge (Edwards Mfg. Co. Model Tru-Chek) at 50 cm.

MICROCLIMATOLOGY

The problems associated with microclimatological investigations in the Arctic have been described by Courtin and Labine (1976) and that explanation serves well to account for the incomplete data recorded in this study. Measurements were confined to several weeks preceeding and after the snow free period.

The instrumentation used, its distribution and the frequency of measurement are outlined in Table 3. A continuous record of all microclimatological parameters was only possible in 1973 and during the following two years, detailed measurements were undertaken only when plant physiological measurements were taken. For possible errors see Appendix [illegible].

INSTRUMENTATION

Global radiation (280-2800 nm) was measured with a Kipp and Zonen Albedometer Model CM-4 at the dry site (1 m). This instrument also measured reflected global radiation and the output from both sensors was recorded at 10 min intervals by a Data Aquisition System (Esterline Angus Model D2020). Reflected global radiation at the moist site was determined with a Kipp and Zonen Solarimeter Model CM-5 mounted upside down at 1 m. The output was recorded continuously for 5 min hr^{-1} on a Portable Strip Chart Recorder (Esterline Angus Model

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T-171-B) equipped with a Stepping Switch (C.P. Clair Canada Division); (see Addison 1973).

Global radiation (350-3500 nm) was recorded on a Robitzsch Bimetallic Strip Pyranograph (Belfort Instrument Co. Model 51850) mounted horizontally at 15 cm.

Table 3. Microclimatological instrumentation, distribution and frequency of measurement on King Christian Island (summer 1973-75).

Station	Sensor	Type of Measurement	Frequency
Lichen-Moss-Rush	Belfort 3-cup Anemometer	wind speed	continuous
	M.C. Stewart Wind Vane	wind direction	continuous
	Belfort Hygrothermograph	air temperature and relative humidity	continuous
	Precipitation Gauge	rain and snow	4 hourly
	Robitzsch-type Pyranograph	global radiation (350-3500 nm)	continuous
	Kipp and Zonen Albedometer	global and reflected radiation (280-2800 nm)	10 min *
	Funk Net Radiometer and Black Body Cup	total incoming radiation	10 min *
	Grant Thermistors	air and soil temperature	hourly
	Thermocouples	near surface temperatures	10 min *
Moss-Lichen-Rush	Belfort 3-cup Anemometer	wind speed	continuous **
	Belfort Hygrothermograph	air temperature and relative humidity	continuous **
	Precipitation Gauge	rain and snow	4 hourly **
	Robitzsch-type Pyranograph	global radiation (350-3500 nm)	continuous **
	Kipp and Zonen Pyranometer	reflected radiation (280-2800 nm)	hourly *
	Grant Thermistors	air and soil temperature	hpurly **
	Thermocouples	near surface temperatures	hourly *

* 1973 only

** 1973 and 1974 only

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Total incoming radiation was determined indirectly with a Funk-type Net Radiometer (Middleton and Co. Model CN-1) with a Black Body Cup attached to the lower surface (1 m). The output (ϕ) was recorded at 10 min intervals on the Data Aquisition System and total incoming radiation (I) was calculated from Equation 1.

$$I = \phi + \epsilon\sigma T_b^4 \qquad (1)$$

where ϵ is the emissivity of the black body cup (1.0), σ, the Stefan-Boltzmann constant (8.17×10^{-11} cal cm^{-2} min^{-1} deg^{-4}) and T_b, the temperature of the black body cup (^oK).

Longwave ($>$2800 nm) incoming radiation (L_d) was calculated from Equation 2.

$$L_d = I - R_T \qquad (2)$$

where R_T is the global radiation (280-2800 nm). It was assumed that owing to the long path-length for global radiation in the Arctic, minimal ultra-violet radiation ($<$280 nm) penetrated to the surface and this component was ignored.

Net radiation (R_n) of the two sites was determined indirectly by calculating R_n of each microsite (Equation 3) and averaging based on the surface area that each microsite contributed to the total.

$$R_n = L_d + R_T - R - \epsilon\sigma T_m^4 \qquad (3)$$

where R is the reflected shortwave (global) radiation, ϵ, the surface emissivity and T_m, the surface temperature. Emissivity

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was assumed to be that of a black body (1.0). An error analysis (see Energy Budget p 52) showed that a 10% decrease in ϵ (0.9 vs 1.0) resulted in a 3% higher value of R_n. Reflected radiation was assumed to be the same for all microsites.

A set of 2-5 thermocouples (0.13 mm diam.) connected in parallel was used to estimate mean surface temperature. Good physical contact between sensor and surface was ensured by imbedding thermocouples into the top mm of bare soil, threading them through lichen thalli and moss stems and mounting them on leaf thermocouple clips for leaves of vascular species. Leaf thermocouple clips (Addison 1973) were modifications of the one used by Fry (1965).

Air and soil temperature at both sites was measured with thermistor probes (Type C) recording on a Grant Model D Multipoint Recorder. The probes were positioned at 25, 10, 5, 2, -2, -15, and -50 cm and all probes above ground were shielded from direct global radiation by self-aspirating aluminum shields (Courtin pers. comm.).

The near-surface temperature profile was determined with 0.075 mm diam. copper-constantan thermocouples at heights of 1, 0.5, -0.5 and -1 cm and referenced at $0^{o}C$ with a cold junction compensator (Omega Engineering Model CJ). Thermocouple outputs were logged on the Data Aquisition

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System at the dry site and the Portable Strip Chart Recorder at the moist site.

A Hair Element-type Hygrothermograph (Belfort Instrument Co. Model 5-594) was used to measure both air temperature and atmospheric humidity. The instrument was enclosed in an aluminum louvered shelter (Vogel and Johnson 1965) and sampled the zone between 10 and 20 cm. A Sling Psychrometer was used to calibrate the Hygrothermograph on a biweekly basis.

Wind speed was measured with 3-cup Totalizing Anemometers (Belfort Instrument Co. Model 5-349) connected to a 10 channel Event Recorder (Esterline Angus Series A). Each mile of wind was recorded as an event and at that time, wind direction was recorded using a Wind Vane (M.C. Stewart Co.) also connected to the recorder. Both Wind Vane and Anemometers were positioned at 50 cm.

Wind profiles were determined with a Hot Wire Anemometer (Hastings-Raydist Model AB-27) and an Omni-directional probe at 4 locations at each site. Measurements were taken at 2, 5, 10, 15, 25, and 50 cm, and 4 sets of readings were taken at each location. Readings were taken 10 sec apart to prevent bias in determining visual means during variable winds (Courtin 1968). All wind profile determinations were carried out when the 50 cm wind speed was between 3 and 5 m sec^{-1} to optimize the sensitivity of the instrument and permit comparisons between prevailing wind directions.

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Precipitation was measured with a Wedge-type Precipitation Gauge (orifice at 35 cm). This instrument has two distinct limitations; it disrupts air flow at the corners hence changing the effective surface area and, it permits small droplets of water to adhere to the sides of the gauge and these are either not recorded or evaporate rapidly. In this study, underestimates of > 50% were observed during light rains (0.08 mm hr^{-1}).

RESULTS AND DISCUSSION

CLIMATOLOGY

The summer climate (1973-75, July and August means) of the Cape Abernathy area, King Christian Island was characterized by low temperature, low precipitation, moderate wind speed and a high incidence of cloud and fog (Table 4). The climate of this area was not unusual and was quite similar to other high arctic sites such as Alert and Isachsen (Table 4). The site had fewer degree days above 0°C than any of the permanent weather stations except Isachsen and even sites as much as 5° in latitude farther north did not have a more rigorous environment. The thermal gradient in the arctic islands appears to be from the polar ice pack towards the Southeast rather than latitudinally. The fact that microclimatological conditions may override the general climatic pattern (Barry and Jackson 1969, Courtin and Labine 1976) means that great care must be taken when estimating conditions at any site from the general synoptic pattern.

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Table 4. Summer (July and August) climatic data from high arctic sites. All values are 1973 and 1974 means. Stations other than Cape Abernathy are from Monthly Record (Atmospheric Environment Service, Canada Department of Environment).

Site	Mean Temperature °C	Precipitation mm	Mean Wind Speed m sec^{-1}	Prevailing Wind Direction	Mean Cloud Cover	Celsius Degree Days above 0°C
Cape Abernathy (77°45'N, 101° 10'W)	2.3	43.0	5.9*	NW	78	141
Alert (82°30'N, 62°20'W)	2.2	49.1	6.2	NE	81	166
Eureka (80°00'N, 85°56'W)	4.2	28.1	5.0	W	76	267
Isachsen (78°47'N, 103°32'W)	2.0	46.0	5.4	SW	86	138
Mould Bay (76°14'N, 119°20'W)	3.1	45.8	5.2	NW	79	197
Rea Point (75°21'N, 94°59'W)	3.0	39.1	7.7	SE	82	193
Sachs Harbour (71°57'N, 124°44'W)	5.0	50.5	7.2	SE	74	315

* Wind speed has been corrected to a height of 10 m after Monteith (1973)

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Although all three years had similar seasonal means of temperature and wind speed, there were great differences in type of season. There was an exceptionally warm and clear spring in 1973 and the land became free of snow very early (June 15, Wittler pers. comm.) whereas in 1974, snow covered most of the area until June 28. Snow and ice remained in a nearby river valley until mid-August in both 1974 and 1975 in contrast with 1973 when this same valley was snow-free by June 25. Maximum, minimum and average weekly mean temperatures (Table 5) showed the same pattern as snow melt, and peaks were reached 10 days later in 1974 than in 1973. The 1975 record is not long enough to compare with the other two years and has only been included to indicate trends.

The greatest difference between 1973 and 1974 appears to be in the amount of cyclonic activity. Comparison of the surface synoptic charts (Atmospheric Environment Service, Canada Department of Environment, Arctic Central Library, Edmonton) with precipitation showed that in almost all cases (95%), precipitation of greater than 0.25 mm occurred when the centre of a low pressure system was within 8 mb of the station. Defining "cyclonic activity" as the time when the centre of a low pressure system was within 8 mb of the station, 39% of the days in 1973 had cyclonic activity as compared with 25% in 1974. It is felt that early snow-melt in 1973 created steep thermal gradients between land and ocean surfaces owing to radiative heating, and permitted greater evaporation.

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Table 5. Weekly means of climatological parameters for summers of 1973 - 1975, Cape Abernathy, King Christian Island.

	Week Ending	Temperature °C MAX	MEAN	MIN	Precip. (mm) AMOUNT	TYPE	Wind(.5m) (m sec^{-1})	R.H. %	Cloud Cover(%)
1973	July 1	4.4	3.6	1.7	.5	S	3.9	100	85
	July 8	12.2	6.8	2.2	5.3	R	3.1	86	47
	July 15	5.5	1.7	0.6	16.8	M	4.2	100	98
	July 22	8.3	2.5	0.3	15.2	M	2.9	100	91
	July 29	6.7	1.8	0.6	2.0	S	3.9	99	89
	Aug 5	8.9	3.8	1.1	0.0	-	3.0	99	75
	Aug 12	8.9	2.6	0.6	3.3	R	3.1	100	97
	Aug 19	6.1	-.2	-1.7	3.8	S	2.6	93	94
	Aug 26	3.3	-.3	-3.9	4.8	S	3.8	99	93
	Sept 2	5.5	1.4	-.6	13.7	R	2.9	100	99
1974	June 10	-1.1	-5.8	-12.2	1.52	S	5.5	91	73
	June 17	3.9	-5.6	-11.1	0.8	S	3.8	87	62
	June 24	5.6	-1.3	-10.0	0.0	-	2.0	83	42
	July 1	4.4	1.3	-2.2	0.0	-	2.5	89	68
	July 8	6.7	1.7	-2.2	9.4	R	3.6	98	97
	July 15	12.2	4.9	0.0	0.0	-	2.9	90	51
	July 22	5.6	2.1	0.0	19.3	M	3.7	98	98
	July 29	7.8	3.1	-.6	1.8	S	3.9	96	60
	Aug 5	7.2	2.7	-1.1	3.1	S	2.9	98	91
	Aug 12	7.2	1.1	-1.6	2.3	S	3.1	96	75
	Aug 19	5.6	2.6	-3.9	3.3	M	4.1	88	73
1975	July 8	4.0	2.9	1.5	0.0	-	-	-	100
	July 15	4.5	1.7	0.0	1.8	M	5.4	93	94
	July 22	5.0	1.9	-.5	6.0	M	3.9	94	87
	July 29	7.5	2.5	0.0	5.1	R	3.5	93	83
	Aug 5	4.0	0.9	-1.5	1.8	M	5.1	95	90
	Aug 12	6.0	2.4	0.0	2.3	R	3.8	92	53

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This would result in greater instability of the atmosphere and hence, greater frequency of cyclones. The differences between the years in precipitation, cloud cover, atmospheric humidity and to some extent wind speed (Table 5) tend to support this hypothesis since all four parameters are at least partially linked to cyclonic activity (Jackson 1961, Müller and Roskin-Sharlin 1967, Lowry 1967, Barry and Hare 1974).

In general, the climate of King Christian Island appears to be dominated by a thermal regime that stems from the heat exchange of land, water and ice surfaces as suggested by Hare (1968) for the entire Arctic. Low temperatures tend to keep relative humidities high since it takes very little water to saturate cold air (Geiger 1966). Both the direct and indirect (humidity) influences of temperature keep evaporation to a minimum; the final result being low precipitation. Although precipitation was low, cloud cover was high and this completed the cycle by reducing the amount of global radiation received and keeping temperatures low. The pattern can be modified however, and the clear and warm spring conditions with high global radiation (1973) was felt throughout the summer. Snow and ice ablation (time and rate) therefore, also appears to be a primary factor in controlling variability of summer climate. The importance of snow and ice in controlling arctic climate has been dicussed by numerous authors (Miller 1956, Marshunova and Chernigovskiy 1966, Barry and Jackson 1969, Bliss et al. 1973).

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MICROCLIMATOLOGY

RADIATION

Global radiation during the summer period showed great variability both between the years studied and throughout the season (Fig 2). In spite of the scatter, a trend of decreasing radiation was evident that corresponded to the pattern on Devon Island (Courtin and Labine 1976). The decline in global radiation over the snow-free period was much greater than that in temperate areas as a result of the rapid decrease in solar altitude after the summer solstice that characterizes polar region radiation regime. The summer (July and August) mean (1973 and 1974) of global radiation (0.21 cal cm^{-2} min^{-1}) was lower than at Truelove Inlet (0.28 cal cm^{-2} min^{-1}, Courtin and Labine 1976), Eureka, Mould Bay, Resolute or Sachs Harbour (0.24, 0.22, 0.22, 0.25 cal cm^{-2} min^{-1} respectively, Monthly Record, AES) but was comparable with values from Alert and Isachsen (0.21 cal cm^{-2} min^{-1}, Monthly Record, AES).

Fig 2 also shows that there was a consistently lower level of global radiation from mid-July to mid-August in 1973 than in either of the other two years presented (ca. 15%). This stems from the greater cloud cover (ca. 15%) and may be related to the greater frequency of cyclonic activity caused by early snow melt (see above).

Global radiation (R_T) is only one component of total incoming radiation (I) (Fig 3) and although it appeared to be

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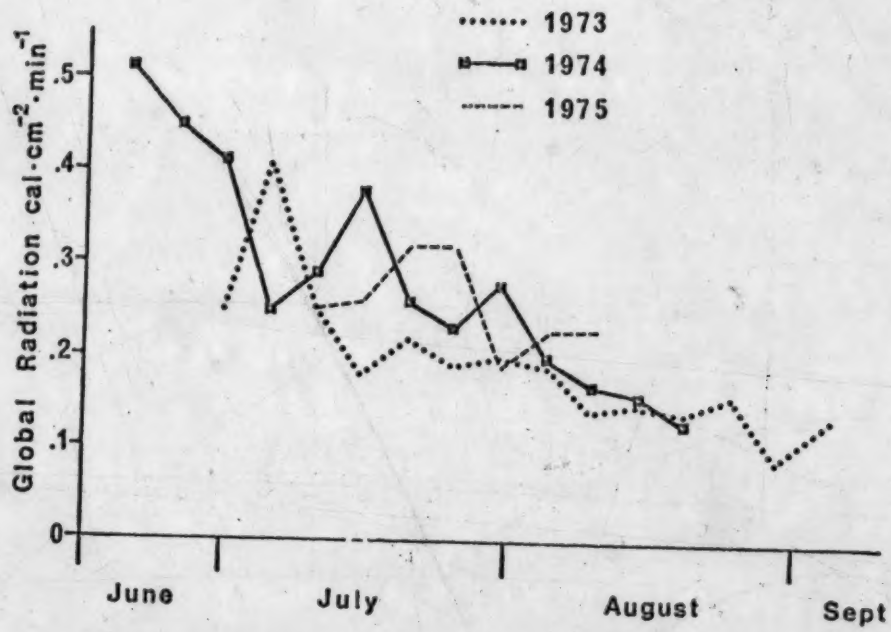

Figure 2. Global radiation during the summer period of 1973 - 1975 at Cape Abernathy, King Christian Island. Values are weekly means.

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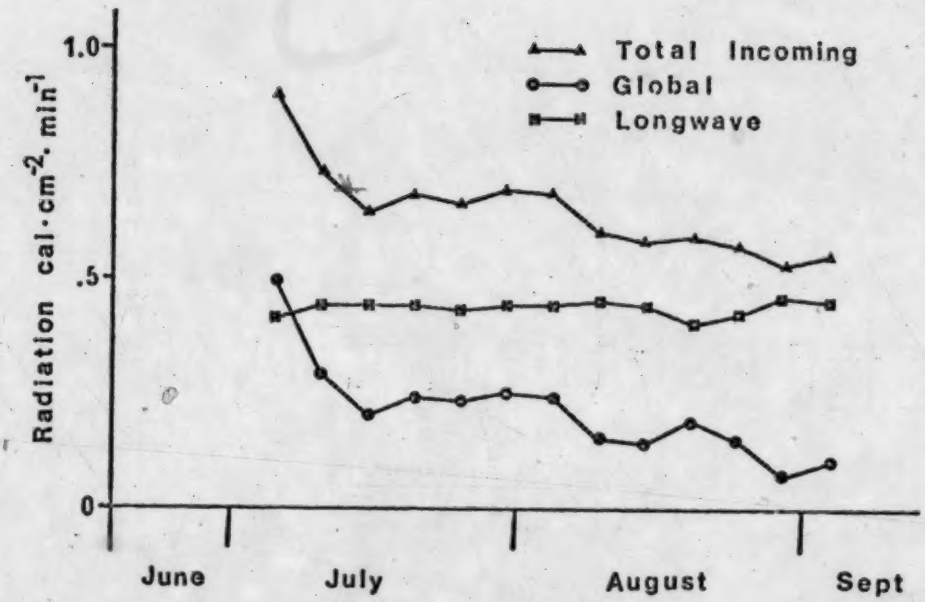

Figure 3. Total incoming radiation and its longwave and shortwave components during 1973. Values are weekly means.

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responsible for variability in total incoming, longwave incoming radiation (L_d) was the major source of radiant energy. During the summer of 1973, Ld exceeded R_T for most of the season and was relatively constant, accounting for 68% of the 0.65 cal cm^{-2} min^{-1} total incoming radiation. Vowinckel and Orvig (1965) estimated that longwave at 78°N should represent approximately 69% of total incoming radiation. Detailed considerations of radiative energy balance are presented under Energy Budget in the following section.

Reflected shortwave radiation was 10% of global radiation at the dry site and 12% at the moist. These albedo values (.10 and .12) remained constant throughout the summer and were comparable with values of .12 to .3 for meadows and fields (Geiger 1966) and other arctic sites (.1 to .4, Jackson 1960, Ahrnsbrak 1968, Weller and Cubley 1972, Addison 1973, Courtin and Labine 1976).

On a seasonal basis, net radiation at the dry site (0.15 cal cm^{-2} min^{-1}) was slightly higher than that at the moist site (0.14 cal cm^{-2} min^{-1}). The difference is within potential instrument error and the values were considered to be the same. Net radiation was 68% of global radiation and 22% of total incoming radiation. These percentages were relatively constant throughout the snow-free period.

Great differences in both albedo and net radiation occurred with snow melt (Fig 4). On June 23 and 24, 1974,

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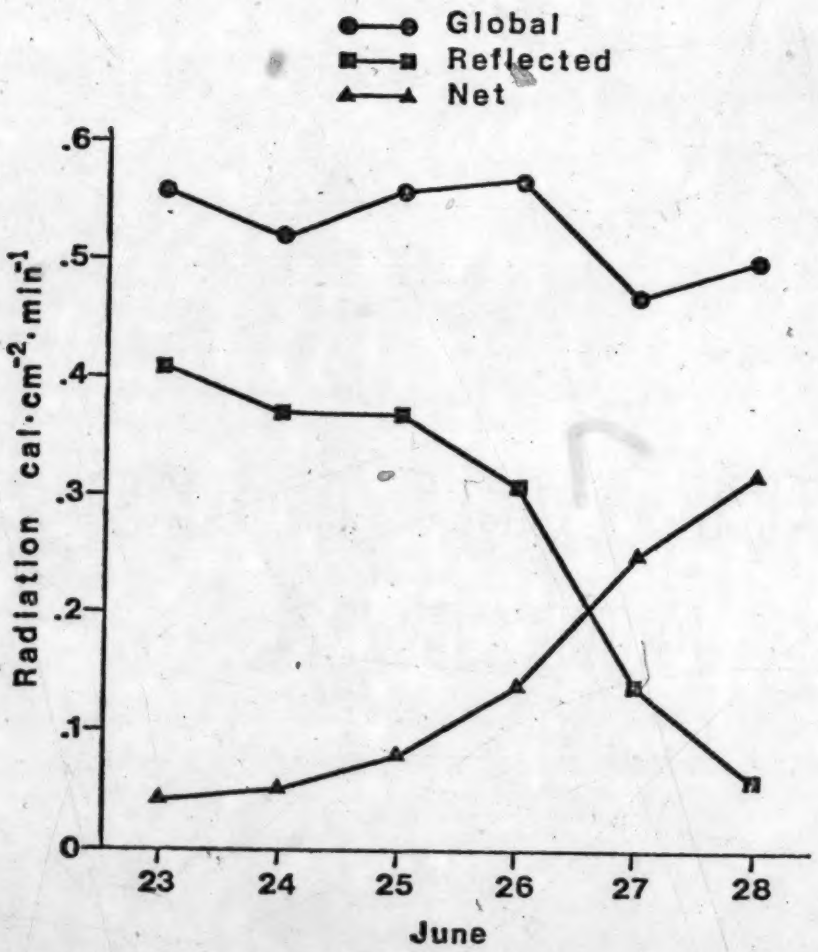

Figure 4. Changes in surface energy regime during snowmelt in 1974. Values are daily means.

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albedo was 0.72 whereas four days later it was only 0.12. This dramatic drop coincided with an increase in absorbed energy that rose from 7 to 64% of global radiation. Snow ablation (19cm in 4 days) was more rapid than was typical at other arctic sites (Weller et al. 1972 and Courtin and Labine 1976). The only exception to this was during adiabatic heating by Föhn winds on Devon Island (Courtin and Labine 1976).

TEMPERATURE

There was great variability in the temperature (1.5 m) throughout the summer seasons of all three years studied (Fig 5) but in spite of this, the seasonal means (July and August) were almost identical ranging from 2.1 to 2.6°C. As at many other arctic sites including Tanquary Fiord, Lake Hazen (Barry and Jackson 1969) and Truelove Inlet (Courtin and Labine 1976), air temperature at 1.5 m increased rapidly following snowmelt. During the snow-free period however, air temperature was correlated with global radiation (r=0.8).

The temperature of the surface of both communities was higher than that at 1.5 m throughout the 1973 summer period (Fig 6). Differences between ambient and the mean of the surface temperatures of the two communities reflected intensity of radiative heating and ranged from 0.8 to 6.2°C (mean 1.7°C). In spite of the differences between ambient and surface temperatures, they were highly correlated (r=0.96),

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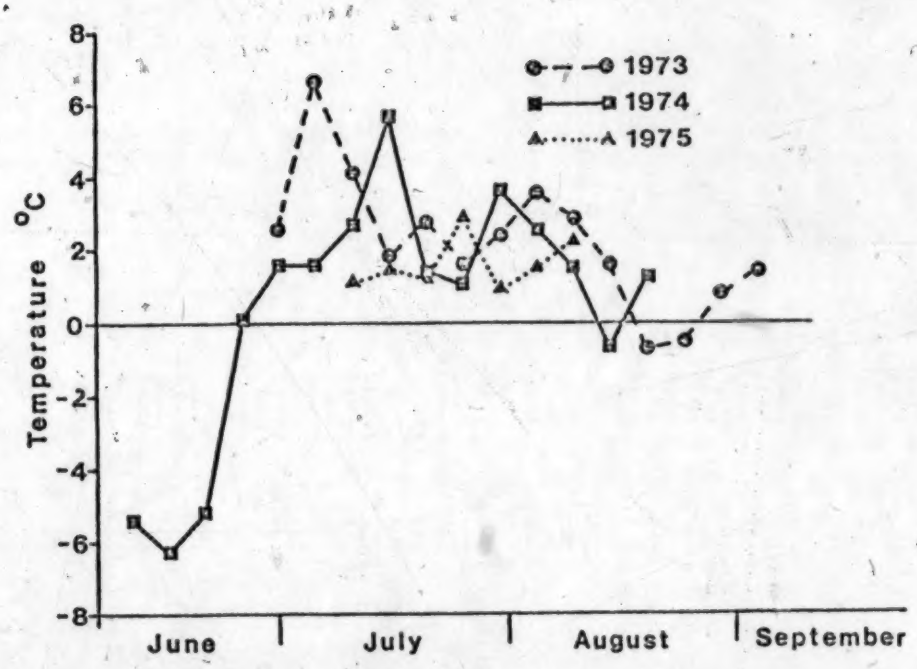

Figure 5. Stevenson screen temperature (1.5 m) during the summers of 1973 - 1975. Values are weekly means.

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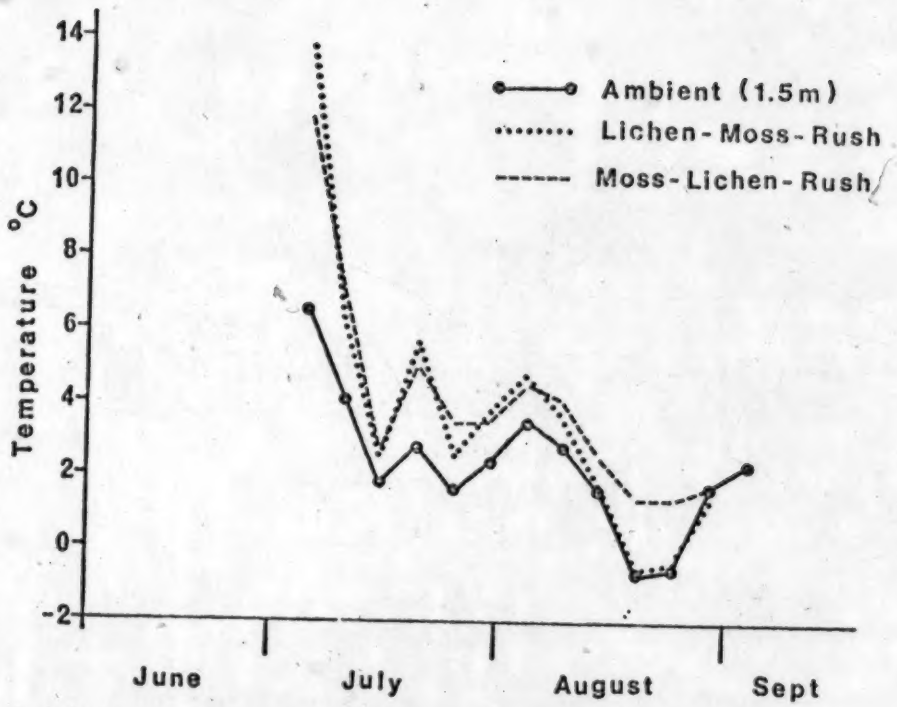

Figure 6. Temperature at 1.5 m and surface of the two plant communities during the summer of 1973. Values are weekly means.

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supporting the hypothesis of Hare (1973) that the lower atmosphere synoptic pattern is controlled by the surface thermal regime.

Fig 6 also shows that although the surface temperatures of the two communities were similar throughout much of the season, they started to diverge in mid-August. This divergence stems from the saturated conditions of the Moss-Lichen-Rush community and the high heat capacity of the water present. The same difference between the sites is also shown in a comparison of the number of celsius degree days at each site in July versus August (Table 6). In July, the Lichen-Moss-Rush surface (dry site) had 70% more degree days than at 1.5 m while the Moss-Lichen-Rush surface (moist site) had only 42% more. In August on the other hand, the dry site had 32% more degree days than at 1.5 m whereas the moist site had 80% more. The lower percentage increase in August than in July at the dry site resulted from lower levels of global radiation whereas the dramatic increase at the moist site resulted from reduced cooling because of high soil water content.

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Table 6. Celsius degree days above 0°C of two plant communities on King Christian Island. Data from 1973.

Month	Height cm	Lichen-Moss-Rush (dry site)	Moss-Lichen-Rush (moist site)
JULY	150	105	105
	10	105	130
	0	178	147
	-5	146	126
AUGUST	150	44	44
	10	44	58
	0	58	79
	-5	35	64

The temperature profiles presented in Figs 7 and 8 show both the influence of the surface heat budget and the seasonal pattern in thermal regime. The curves are 5-day means in 1973 representing periods of high (ending July 8), moderate (ending Aug 1) and low (ending Aug 27) insolation (0.39, 0.27, 0.09 cal cm^{-2} min^{-1} global radiation respectively).

The greatest difference in the profiles at the dry site was in the amount of surface heating. Under high radiation the temperature gradient from 0 to 5 cm was 3 C° whereas under moderate insolation it was 1.3 C° and under low insolation 0.9 C°. The moist site on the other hand, showed little surface heating (< 0.5 C°) under all light conditions.

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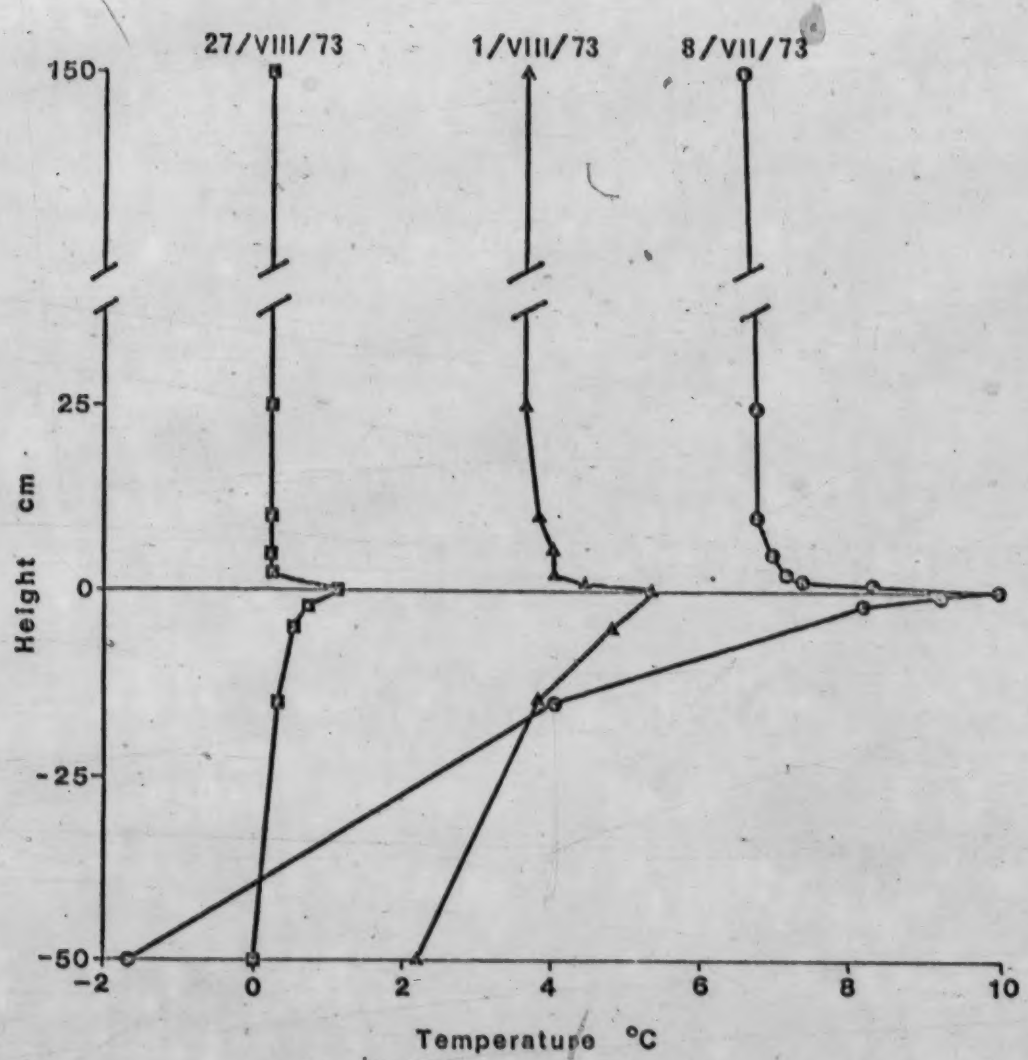

Figure 7. Temperature profiles at the Lichen-Moss-Rush community for selected periods in 1973. Values are 5 day means.

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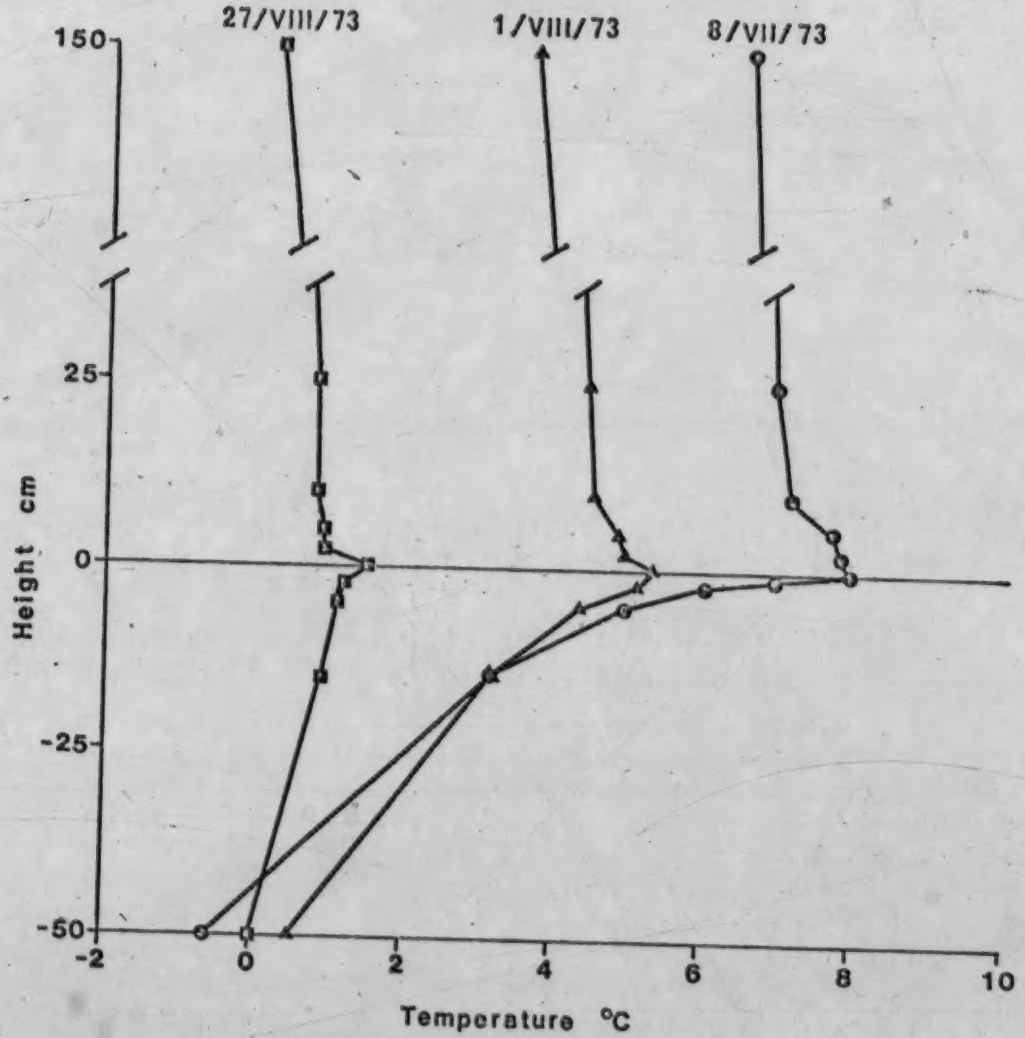

Figure 8. Temperature profiles at the Moss-Lichen-Rush community for selected periods in 1973. Values are 5 day means.

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Surface water, its high heat capacity and its influence on latent heat flux appears to account for the difference between sites since R_n of both was the same.

The thermal gradient in the top 2 cm of soil was steeper at the moist site than at the dry one. The difference appears to stem from both differences in heat capacity and thermal conductivity between the sites. Thermal conductivity of peat is much less than that of mineral soil (0.1 - 1.2 vs. 0.7 - 5.4 millical cm^{-1} sec^{-1} deg C^{-1}; van Wijk 1965) and since the moist site had a much greater cover of moss (ca. 2 cm deep), the thermal conductivity of the surface layer should be less at the moist site than at the dry site. There was also less seasonal amplitude in temperature (-50 cm) at the moist site supporting the hypothesis of lower conductance at this site.

The seasonal trend in thermal regime is reflected in the temperature gradient in the soil (Figs 7 & 8). In early summer (July 8), the temperature gradient (0 to -50 cm) was extremely steep (ie. 11.6 C^o, dry site and 8.5 C^o, moist site). This gradient decreased throughout the season and approached zero on August 27. Since the temperature at -50 cm on Aug 27 was lower than on Aug 1 at both sites, it can be expected that the active layer was decreasing in depth. Direct measurements of active layer depth showed an 8 cm decrease from August 5 to August 25, 1973 at both

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sites. The maximum soil thaw in 1974 also occurred in mid-August (between Aug 12 and 20) reaching a depth of 48 cm at the dry site and 49 cm at the moist site; about 3 cm less than in 1973. The time of maximum active layer depth appears to be related to latitude and it is earlier as one goes north. Cape Abernathy had one of the earliest times of maximum soil thaw reported (Table 7).

Table 7. Time of maximum active layer depth of some arctic sites.

Site	Latitude	Time of maximum active layer	Author
Eureka	80°N	Mid-August	Smith (1975)
Cape Abernathy	78°N	Mid-August	This study
Resolute	75°N	End August	Cook (1955)
Truelove Inlet	75°N	Early September	Courtin and Labine (1976)
Barrow, Alaska	71°N	Mid-September	Mather and Thornthwaite (1956)
Abisko, Sweden	68°N	November	Skartveit et al. (1975)

WIND

Wind speed at Cape Abernathy was moderate and averaged 3.3 m sec^{-1} at 50 cm both in 1973 and 1974 (Table 5). This value can be used as an average for the entire area since there were no major topographic features to influence either speed or direction such as occur at Tanquary Fiord (Barry and

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Jackson 1969) or Truelove Inlet (Courtin and Labine 1976). Prevailing winds were from the northwest but winds from both north and south were frequent (ca. 20%), (Fig 9).

Rae (1951) pointed out that wind speed in the Arctic was no greater than in temperate areas but that its effect may be greater because of the relatively smooth tundra surface. The wind profiles (Fig 10) confirm this and the roughness length (z_o) of the two communities (moist and dry) were 0.015 and 0.024 cm respectively. These values (.005 to .05 cm) are much lower than reported for vegetated surfaces (eg. 0.1 cm, grass; 4 cm, Barley and 20 cm, maize; Monteith 1973) but similar to that of smooth snow (0.01 cm, Weller et al. 1972). Using the relationship of Tanner and Pelton (1960) and Stanhill (1969) given by Monteith (1973, p 88-90), the zero plane displacement (d) for both communities was calculated to be 0.08 cm. This means that the influence of wind was felt almost to the surface resulting in low air resistance to water and heat flux from the surface.

PRECIPITATION

Precipitation at Cape Abernathy, King Christian Island, was comparable with that at other sites close to the polar ice pack (Alert, Isachsen and Mould Bay; Table 4). Fig 11 shows the seasonal distribution of precipitation and although there may be large errors in the data (see Methods), two points are clear. There was a greater amount and a higher frequency of

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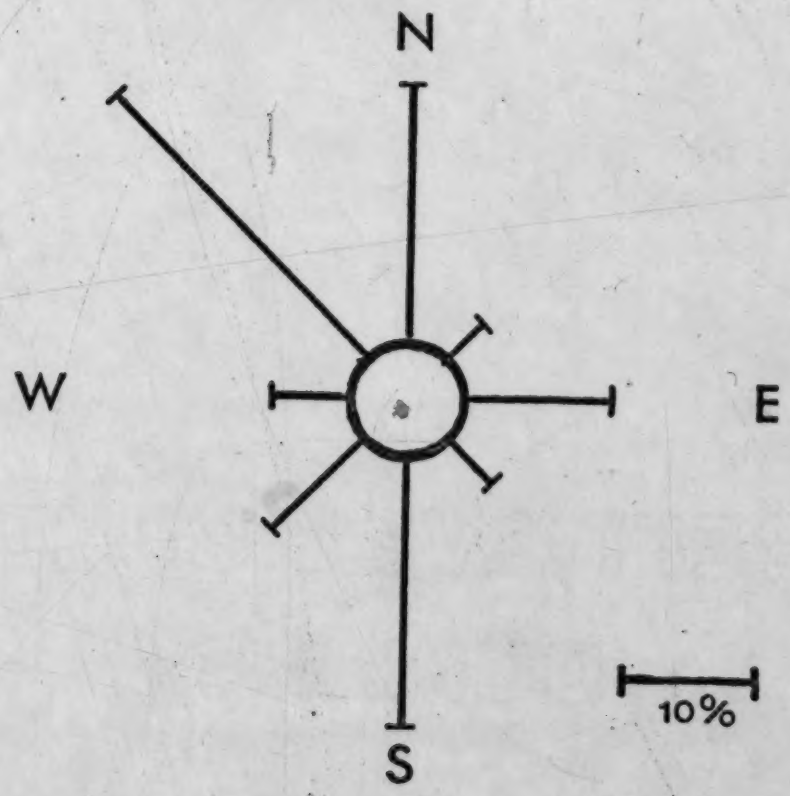

Figure 9. Wind direction rose indicating the frequency (%) of winds from various directions at Cape Abernathy, King Christian Island (summers 1973 - 74).

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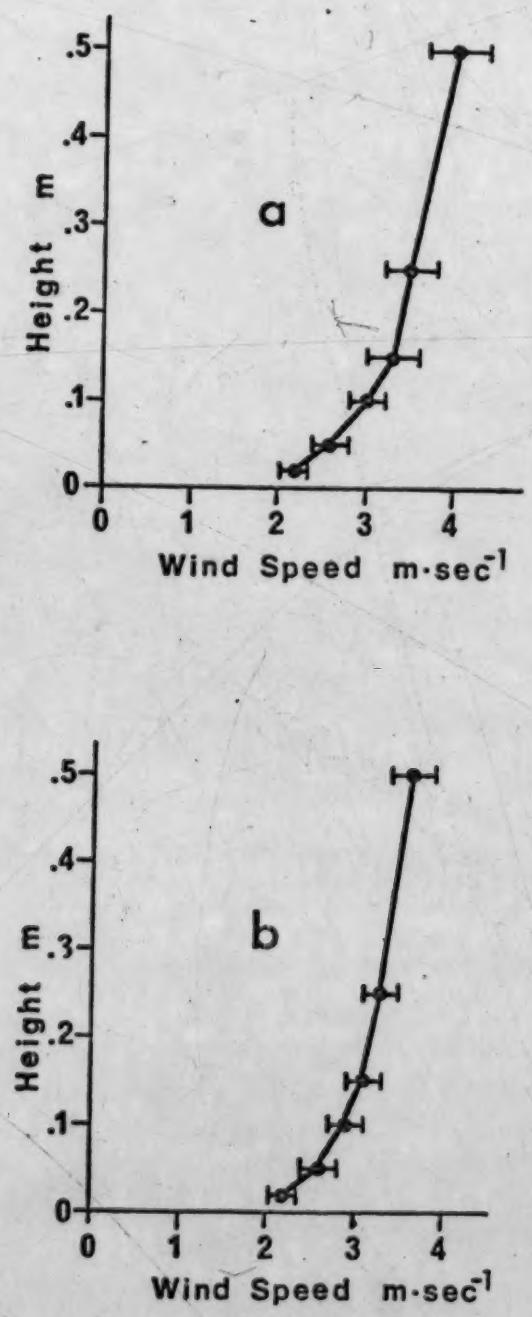

Figure 10. Wind profiles during periods of moderate wind speed (3-5 m sec^{-1} @ 50 cm) at the Lichen-Moss-Rush (a) and Moss-Lichen-Rush (b) communities. Values are means ± 95% confidence limits.

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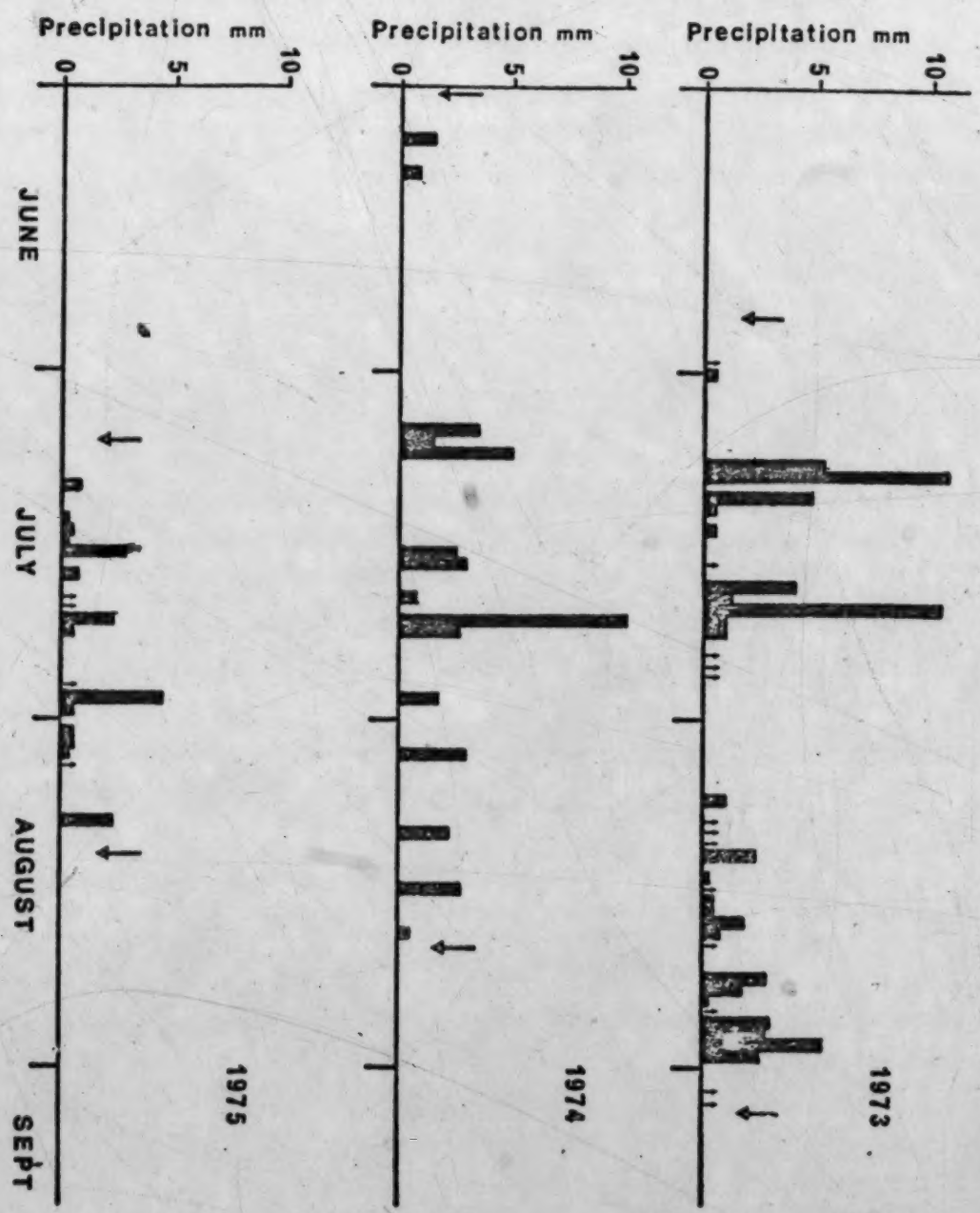

Figure 11. Summer precipitation on King Christian Island (1973 - 75). Arrows mark the ends of the measurement period and values are water equivalent.

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precipitation in 1973 than in either 1974 or 1975 as mentioned before (Climatology) and there was a period of low precipitation just before and during snow-melt in 1974. This period may correspond to the sunny, early spring period on Devon Island (Courtin and Labine 1976) but it occurred a month later. Observations were not sufficiently long-term however, to make generalizations.

CONCLUSIONS

In general, the summer climate of King Christian Island is typical of the North and Northwest Queen Elizabeth Islands as evidenced by the similarity to Alert, Isachsen and Mould Bay. All of these sites are in close proximity to the polar ice pack and it is felt that the thermal gradient in the arctic islands is from this ice pack to the southeast. All climates are characterized by cool temperature , low precipitation, moderate wind speed, high relative humidity and a high frequency of low clouds or fog.

The two plant communities had similar above-ground microclimates except very close to the ground surface. The similarity stems from both the limited size of the sites as it relates to fetch requirements, and the smooth surfaces that permitted turbulence almost to the surface thus dissipating gradients of heat and moisture.

The below-ground environments on the other hand, were quite different and the Moss-Lichen-Rush community was

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cooler and more moist than the Lichen-Moss-Rush community for most of the growing season. By the time that the moisture conditions at the Moss-Lichen-Rush ameliorated the soil thermal regime, many of the plants had ceased growth and hence, the improved conditions may have very little biological significance.

The major reason for describing the microclimates of the two plant communities was to permit expansion of plant physiological processes to ecologically meaningful relationships. Since microclimate is only one component of the holocoenotic environment, the implications of this part of the study have been left until all components can be presented (see Ecological Implications p 135).

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ENERGY BUDGETS

INTRODUCTION

Studies of energy balance in arctic and alpine areas have been extremely rare even though there have been many proponents of the approach (Gates 1962, Hare and Ritchie 1972, Hare 1973). The rigorous conditions in these areas hamper the maintenance of the required complex instrumentation resulting in the paucity of data. Energy budget studies have been carried out by Terjung et al. (1969) and LeDrew (1975) in alpine areas and by Weller et al. (1972), Haag and Bliss (1974), Weller and Holmgren (1974), Smith 1975) and Addison (1976) in the Arctic. The energy budget approach permits explanation of the thermal regime, one of the major factors controlling plant growth in these rigorous environments.

METHODS AND MATERIALS

The methods used to determine the radiation balance at the surface have been outlined above (see Microclimatology p 19).

Spectral quality of global radiation was determined under both clear and cloudy conditions with a Spectral Radiometer (I.S.C.O. Model SR) at selected times during 1975. This instrument was also used to determine the spectral quality of global radiation on a diurnal basis in the field and in

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environmental growth chambers in the laboratory. In addition to spectral radiometer measurements, photosynthetically active radiation (PAR; 400 - 700 nm) was measured with a Quantum Sensor (Lambda Instruments Model LI-190SR) when photosynthetic and respiration rates were determined in 1975.

Absorbed or net radiation (R_n) can be defined as the difference between incoming and outgoing radiation (Equation 3; Microclimatology p 21) or the sum of the non-radiative energy fluxes:

$$R_n = LE + H + G + M \qquad (4)$$

where L is the latent heat of vapourization (580 cal g^{-1} @ 20°C); E, rate of water loss (g cm^{-2} min^{-1}); H, sensible heat flux; G, soil heat flux and M, plant metabolic energy flux. M is usually small (< 2%, Reifsnyder and Lull 1965) and because of sparse plant cover (5 - 15%), was ignored. The units of R_n, H, G and M are cal cm^{-2} min^{-1}.

Water loss from each microsite was measured directly with sod blocks 8.25 cm in diameter and 11.5 cm deep. Sod blocks were positioned so that the top of the block was flush with the ground surface, and measurements were made by removing and weighing them on a triple-beam balance (± 0.1 g). The balance was housed in a plastic shelter or a tent to permit accurate field measurements regardless of weather conditions. In the case of the vascular plant

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microsites, sod blocks with dead plants were also weighed to permit separation of the evaporational and transpirational components of evapotranspiration. Duplicate sod blocks were used in all cases and measurements were taken every 4 - 12 hr in the summer of 1973 and every 2 hr while plant physiological parameters were monitored in 1974 and 1975.

Soil energy flux (G) was measured with Heat Flux Plates (Middleton and Co.) placed 1 cm below and parallel to the surface. These plates measured the rate of energy transfer through the soil beneath the Luzula, moss, lichen and bare soil microsites of both plant communities. Heat flux was assumed to be the same for all vascular plants. The output from these plates was recorded on the Data Aquisition System at the Lichen-Moss-Rush community (10 min intervals) and on the Portable Strip Chart Recorder at the Moss-Lichen-Rush community (5 continuous minutes per hour). Sensible heat flux (H) was determined from Equation 4 since all other variables were known.

RESULTS AND DISCUSSION

The major components of the radiation balance were the longwave fluxes (Table 8). Longwave incoming radiation contributed 68% of total incoming radiation; slightly more than on Devon Island (65%; Addison 1976). These values corresponded closely to theoretical calculations of longwave flux (69%) by Vowinchel and Orvig(1969). The empirical model

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of Monteith (1973) estimated incoming longwave radiation that was essentially identical to the measured value (.443 vs .441 cal cm^{-2} min^{-1}). Estimates by the model of Geiger (1966) on the other hand, were about 18% lower than measured (.361 vs .441 cal cm^{-2} min^{-1}). The high percentage contribution by longwave radiation to total incoming radiation in polar regions results from both the high incidence of low clouds and the greater atmospheric pathway that decrease global radiation. Reradiative flux accounted for 74% of total incoming; only 4% was reflected and 22% was absorbed.

No attempt was made to account for reflected longwave radiation since it was not possible to measure it with the instruments available. This means that the presented net radiation may be somewhat lower than actual. If the actual emissivity of the surface was 0.9 rather than 1.0 (assumed), net radiation would be 0.147 cal cm^{-2} min^{-1} or 3% higher. This magnitude of error is insignificant compared with the potential error in measurement (see Appendix B).

Photosynthetically active radiation (PAR; 400-700 nm) averaged 50.2% of global radiation (R_T) based on measurements taken with the spectroradiometer during the summer of 1975. A linear regression between PAR (Quantum Sensor) and R_T (Albedometer) was determined (PAR in μE m^{-2} sec^{-1} = 0.125 + 1604.6 x R_T in cal cm^{-2} min^{-1}; r=.998) and permitted an estimate of PAR from global radiation for the July 15 to August 14, 1973 period.

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Table 8. Radiation regime of the Cape Abernathy region, King Christian Island. Values are averages from July 15 to August 14, 1973.

RADIATION	RADIATION, cal cm^{-2} min^{-1}	% INCOMING	% GLOBAL
Incoming (all wave)	.649	100	
Longwave (>2800 nm)	.440	68	
Global (280-2800 nm)	.209	32	100
Reradiated (>2800 nm)	.483	74	
Reflected (280-2800 nm)	.024	4	11
Net (all wave)	.142	22	68
Visible (400 - 700 nm)*	.105		50

* Values are based upon spectroradiometer measurements in 1975 and global measurements of 1973 (see text)

The spectral quality of global radiation (Fig 12) was very similar to that in the Oregon alpine (Curl et al. 1972) with a peak at 450 nm and a rapid decline from 550 to 750 nm. This is somewhat different than the spectrum on Devon Island where the decline from the peak at 475 nm was much less dramatic and there was a greater proportion of radiation in the longer wavelengths (550 - 750 nm); (Mayo et al. 1972). Both low sun angles (Fig 12) and cloud cover (Fig 13) resulted in a greater reduction in short wavelengths (450 - 600 nm) than in longer ones (600 - 750 nm) hence increasing the proportion of red and far red light under these conditions. A similar shift in the proportion of blue and red light has been reported from Devon Island (Mayo et al. 1976). The spectrum of radiation on King Christian Island also had peaks

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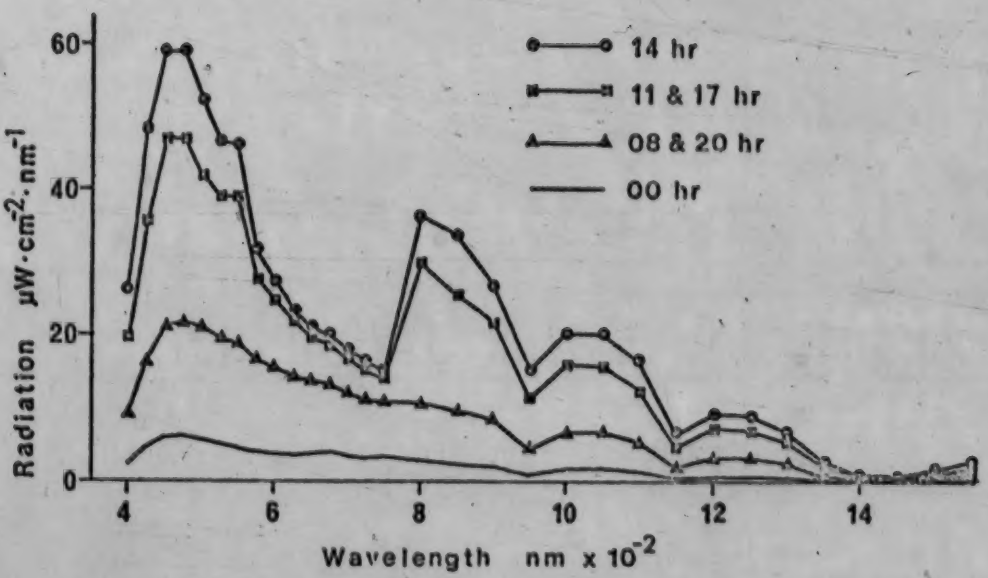

Figure 12. Spectrum of global radiation at selected times on August 6, 1975.

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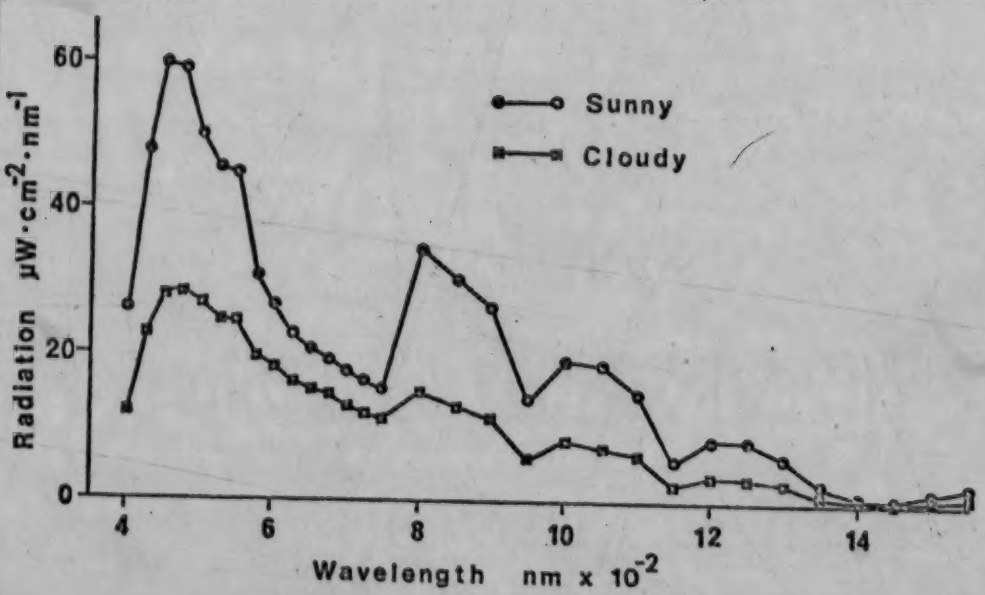

Figure 13. Spectrum of global radiation at 1645 hr during clear (July 23, 1975) and cloudy (July 25, 1975) conditions.

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at 800, 1000, and 1200 nm similar to Devon but they were much more pronounced on King Christian.

Teeri (1974) suggested that flowering of Saxifraga rivularis may be controlled by a shift in the red to far red ratio (phytochrome response). Field measurements of red to far red ratios (1.2 - 1.3) on King Christian Island corresponded to those on Devon Island (1.1 - 1.8; Mayo et al. 1976) and there was no shift during the three week period of measurement (Table 9). There was also no measureable shift in red to far red ratio with time of day (Table 10). Since the measurement of red to far red ratios spanned the time when vascular plants commenced die back in the field, it is unlikely that the classical 660 - 730 reaction of phytochrome is involved as a mechanism in biological timing. It may be however, that the dramatic reduction in blue light results in a "physiological" night that has the same influence as Biebl (1967) showed for short days (Mayo pers. comm.).

Table 9 Red to far red ratios at selected times during the summer of 1975.

DATE	TIME	SKY CONDITION	RED TO FAR RED 660:730 nm
July 15	1700	Clear	1.29
July 17	1700	Clear	1.30
July 20	1700	Clear	1.30
July 23	1700	Clear	1.28
July 24	1700	Clear	1.30
July 25	1700	Overcast	1.28
July 31	0800	Clear	1.21
Aug. 6	1700	Clear	1.30

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Table 10. Diurnal variations in red to far red ratio under clear sky conditions (Aug 6 and 7, 1975).

TIME	RATIO	TIME	RATIO
0800	1.26	1600	1.24
0900	1.29	1700	1.30
1000	1.30	1800	1.29
1100	1.30	1900	1.28
1200	1.31	2000	1.24
1300	1.30	2200	1.26
1400	1.30	0000	1.20
1500	1.30		

Calculated net radiation of all microsites of the Lichen-Moss-Rush community was higher than microsites in the Moss-Lichen-Rush community (Table 11). The difference stems from both greater reflectivity and greater reradiation by the Moss-Lichen-Rush community. Greater reflectivity appears to be related to the presence of surface water and after rain, when surface water was present at both sites, reflected radiation was the same. The Moss-Lichen-Rush community reradiated more energy than the Lichen-Moss-Rush community (0.49 vs 0.48 cal cm^{-2} min^{-1}) because of the higher surface temperature (4.7 vs 3.5 ^{o}C). Differences in R_n among the microsites at each site appeared to result from surface temperature differences since reflection from all parts of each site was assumed to be identical.

Latent heat flux was the same at both sites even though one site (Moss-Lichen-Rush) had surface water present for most of the season and the other did not. The influence of surface conditions on water loss (E) was quantified by calculating

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Table 11. Net radiation and its components of microsites at each of the two plant communities. Values are averages from July 15 to August 14, 1973 and units for energy fluxes are cal cm^{-2} min^{-1}.

SITE	MICROSITE	R_n	LE	H	G	TEMPERATURE °C
LICHEN -MOSS -RUSH	LUZULA	.147	.029	.112	.006	3.67
	POTENTILLA	.147	.032	.109	.006	3.68
	SAXIFRAGA	.149	.026	.117	.006	3.36
	MOSS	.144	.024	.108	.012	4.13
	LICHENS	.149	.041	.086	.022	3.36
	BARE SOIL	.150	.043	.085	.022	3.33
ENTIRE SITE		.148	.038	.091	.019	3.51
MOSS- LICHEN -RUSH	LUZULA	.139	.049	.070	.020	4.20
	POTENTILLA	.143	.040	.083	.020	3.76
	MOSS	.136	.039	.087	.010	4.64
	LICHENS	.134	.034	.084	.016	4.99
	BARE SOIL	.140	.048	.067	.025	4.09
ENTIRE SITE		.136	.038	.084	.014	4.71

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the resistance (R_w) that the surface imposes on the flux (Equation 5: Slatyer 1967, p 247).

$$E = \frac{273}{P\,T}\,\rho\,\frac{(e_s - e_a)}{R_w} \qquad (5)$$

where P is atmospheric pressure; T, air temperature (°K); ρ, density of water vapour (g cm^{-3}) and e_s and e_a the vapour pressure of water at the surface and in the air respectively. All pressures are in mm Hg. The resistance to water loss for all microsites was 0.37 sec cm^{-1} for the Lichen-Moss-Rush and 0.36 sec cm^{-1} for the Moss-Lichen-Rush. Based on the mean wind speed for the period (3.1 m sec^{-1}) and using the relationship of resistance versus boundary layer thickness (Slatyer 1967, p 248), the resistance to water flux of both sites represented a boundary layer thickness of 0.09 cm. This value corresponds closely with the zero plane displacement of the canopies (0.08 cm) as given by the wind profile measurements (see Microclimatology p 42) and hence, both surfaces respond like freely evaporating water at the base of the canopy. There was little or no surface drying since that would have increased the resistance substantially. It appears therefore, that the low latent heat flux (i.e. 27% of R_n) was caused by the very shallow vapour pressure gradient between surface and air because of cool temperature and high relative humidity.

The resistance of the earth's boundary layer to sensible heat flux (R_t) was also calculated using the method of Slatyer

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(1967, p 243) and estimates of H determined from Equation 4. R_t was 0.20 and 0.16 sec cm^{-1} for the Lichen-Moss-Rush and the Moss-Lichen-Rush communities respectively. It appears therefore, that the fluxes of both heat and water are near maximum for the gradient present because of the smooth surfaces that have thin boundary layers and hence, low resistance to flux.

The major difference among the microsites at each site was in soil heat flux (G). Vascular plant and moss microsites of the Lichen-Moss-Rush community significantly reduced G as compared with lichen and bare soil microsites ($p<.05$, Student-Newman-Keuls test; Sokal and Rohlf 1969, p 240). It is likely that buildup of surface organic matter at vascular plant and moss microsites was responsible for the reduction of G.

At the Moss-Lichen-Rush site, vascular plants and bare soil microsites had significantly greater soil heat fluxes than either of the two non-vascular plant microsites ($p < .05$). It is felt that this may be related to soil moisture conditions rather than organic matter buildup but it was not possible to distinguish between the two.

In general, soil heat flux of the Lichen-Moss-Rush community was greater than that of the Moss-Lichen-Rush community mainly owing to a higher percentage cover of bare soil that had the greatest G of all microsites.

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Only the vascular plant microsites showed a significant difference between sites ($p < .05$) but no explanation for this difference was possible with the data collected.

Net radiation (R_n) and its components for several arctic and alpine sites are presented in Table 12. It was not possible to make specific comparisons of R_n between sites because R_n is controlled by the radiation regime which in turn depends on type of year and local climatic conditions. In general however, R_n of the King Christian Island site was quite similar to monthly means of other arctic areas. The data of Addison (1976) and Terjung et al. (1969) show that specific climatic conditions on relatively few days may result in net radiation values that are not necessarily typical of the summer period. Although plant survival and growth appear to be controlled more by summer rather than winter conditions (Billings 1974), it is the entire yearly radiation budget that can be correlated with the boundaries of vegetation formations (Hare and Ritchie 1972). This means that even though summertime radiation balance studies are useful for determining the growing conditions of plants, yearly studies such as those of Wendler (1971) and Courtin and Labine (1976) are necessary in order to understand overall climate and hence aid in an explanation of plant distribution.

Latent heat flux appears to be controlled by availability of surface water in all but the present study

Table 12. Net radiation and its components of several arctic and alpine sites during July.

LOCATION	R_n cal $cm^{-2} min^{-1}$	% of R_n LE	H	G	MEASUREMENT PERIOD	AUTHOR
Alpine meadow 37°34'N, 118°14'W	.382	60	29	11	11 hrs	Terjung et al. 1969
Alpine meadow 40°03'N, 105°35'W	.207	38	50	12	Month	LeDrew 1975
Low Arctic meadow 70°45'N, 156°00'W	.199	40	52	8	Month	Mather 1958
Low Arctic meadow 70°45'N, 156°00'W	.165	66	32	2	14 days	Weller and Holmgren 1974
Low Arctic meadow 64°50'N, 147°40'W	.116	85	3	12	Month	Wendler 1971
Low Arctic shrub 64°50'N, 147°40'W	.099	57	33	10	Month	Wendler 1971
Low Arctic shrub 69°27'N, 133°00'W	.146	56	25	19	Month	Haag and Bliss 1974
High Arctic meadow 74°40'N, 84°40'W	.243	53	37	10	4 days	Addison 1976
High Arctic Semi-desert Gravel Ridge 74°40'N, 84°40'W	.214	21	70	9	4 days	Addison 1976
High Arctic Semi-desert Sandy loam lowland 77°45'N, 101°10'W	.142	27	62	11	Month	Present Study

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where low air temperatures and high relative humidities prevailed. The proximity of the polar ice pack and the general air flow from ice pack to King Christian Island appears to be the dominant feature in maintaining the low temperature and high relative humidity.

Soil heat flux (G) of most sites dissipated 8 - 12% of R_n and surprisingly, appeared to be rather independent of the type of vegetative cover. It is appreciated however, that total removal of vegetative cover results in a greater G and hence, greater active layer depth (Haag and Bliss 1974, Smith 1975). Removal of vegetation at this site increased active layer depth by 9 cm in 1974 (55 cm vs 46 cm control).

Because of great variability among the sites and the limited number of energy budget studies, no comparison between arctic and alpine sites was possible.

CONCLUSIONS

Longwave radiation fluxes were the major components of the surface radiation balance and can be accurately estimated if the surface and air (1.5 m) temperatures are known. Net radiation was 22% of total incoming or 68% of global radiation and in general, was comparable with other arctic sites.

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The components of net radiation for a month period in mid-summer were LE (27%), H (62%) and G (11%). The low LE term appears to result from near-surface atmospheric conditions (low temperature and high relative humidity). There was little resistance to water flux because of both the smooth community surface (i.e. thin turbulent boundary layer) and the high moisture conditions in the upper soil layers. Soil heat flux was greater for non-vegetated surfaces than for vegetated ones and removal of surface vegetation resulted in a 19% greater active layer thaw.

Red to far red ratios were relatively constant (1.2-1.3) during the time when vascular plants started winter preparation (die-back or leaf colouration). This suggests that the classical 660-730 reaction of phytochrome is not involved in controlling the length of the growing season. Shifts in blue light may be important at this latitude.

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SOILS

INTRODUCTION

Recent work on arctic soils has involved mainly classification (Tedrow 1966, C.S.S.C. 1973), mapping (Tedrow et al. 1968, Walker and Peters 1976) or soil pedogenic processes (Tedrow and Brown 1962, Retzer 1965). In addition, many studies have used generalized climatic, vegetational or topograghic features to delimit soils in Polar Desert and Polar Semi-desert areas (Charlier 1969, Bovis and Barry 1974). Since the present study had a botanical frame of reference, only a limited amount of soil work was attempted to 1) describe the soil in sufficient detail to permit classification and comparison with other high arctic sites and 2) describe the soil moisture regime in the light of requirements for plant growth.

The soil thermal regime has been discussed above (Microclimatology p 34) and for nutrient analyses see Bell (1975).

METHODS AND MATERIALS

Observations from 8 soil pits dug at each of the two plant communities followed the categories as outlined in The System of Soil Classification for Canada (C.S.S.C. 1974). Soil texture was determined using the hygrometer technique for the sand, silt and clay fractions (Bouyoucos 1951).

In 1973, soil water potential was monitored with soil psychrometers (Wescor Inc.) but owing to cold and moist soils

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and very steep thermal gradients in the upper part of the soil (see Microclimatology p. 34), these instruments failed to yield reliable results. Soil water content was determined gravimetrically on a weekly basis in 1974 and 1975. Detailed measurements of soil moisture (4 hourly) were also taken during the periods when plant physiological processes were monitored. In all cases, duplicate samples were taken at 0 - 5 and 10 - 15 cm depths and all samples were dried at approximately 80°C for 24 - 48 hr.

In order to convert soil moisture (gravimetric method) to soil matric potential, water retention curves of the <2 mm fraction were determined. A pressure plate apparatus (Soil Moisture) was used and soil water content at 1/3, 1, 2, 5, 8 and 15 bars was determined gravimetrically. Water retention curves were determined for soils at 4 locations and at 4 depths (0-5, 5-10, 10-15, and 15-20 cm) at each site.

RESULTS AND DISCUSSION

Soil pedons from both the Lichen-Moss-Rush and the Moss-Lichen-Rush communities were morphologically identical and had no horizonation. The area was very gently sloping, gullied land (E1) that was imperfectly to poorly drained. Only a "C" horizon (undifferentiated parent material) was present and it was very dark grayish brown (2.5 Y 3/2 m) or grayish brown (2.5 Y 5/3 d); very fine sandy loam; amorphous; friable; very fine, random roots; abundant, very fine random pores; 45 cm thick; pH 6.0. There was an abrupt, smooth boundary at ca.

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45 cm to the "Cz" horizon. Pawluk and Brewer (1975) indicated that the soils of the area had some development based on micromorphological and analytical characteristics, and suggested that they should not be considered regosolic. Following the pedon concept (Soil Survey Staff 1960) as specified for northern soils (C.S.S.C. 1973) and based on profile morphology, the soil was considered regosolic. The soil therefore, was a Regosolic Static Cryosol (C.S.S.C. 1973) or a Pergillic Cryaquent (Soil Survey Staff 1967). The soil was quite similar to many that have been described from other Polar Desert and Polar Semi-desert areas (Tedrow et al. 1968, Tedrow 1970, Cruickshank 1971, Walker and Peters 1976).

Soil moisture (0-5 cm) of both sites ranged from 15% to 25% of oven dry weight throughout the summers of 1974 and 1975 (Fig 14) and there was a slight decline as the season progressed. Water content at the Lichen-Moss-Rush community was higher in 1975 than in 1974 and it appears that this was linked to frequency of precipitation rather than total amount (Fig 11). Based on this, it follows that soil moisture in 1973 would have been intermediate to the two years presented. The similarity between the years at the Moss-Lichen-Rush community stems from poor drainage. All values of water content during 1974 and 1975 were either above or close to field capacity (1/3 bars; Fig 15). Soil moisture below 5 cm was above field capacity throughout the summer season and followed the same pattern as the 0-5 cm depth.

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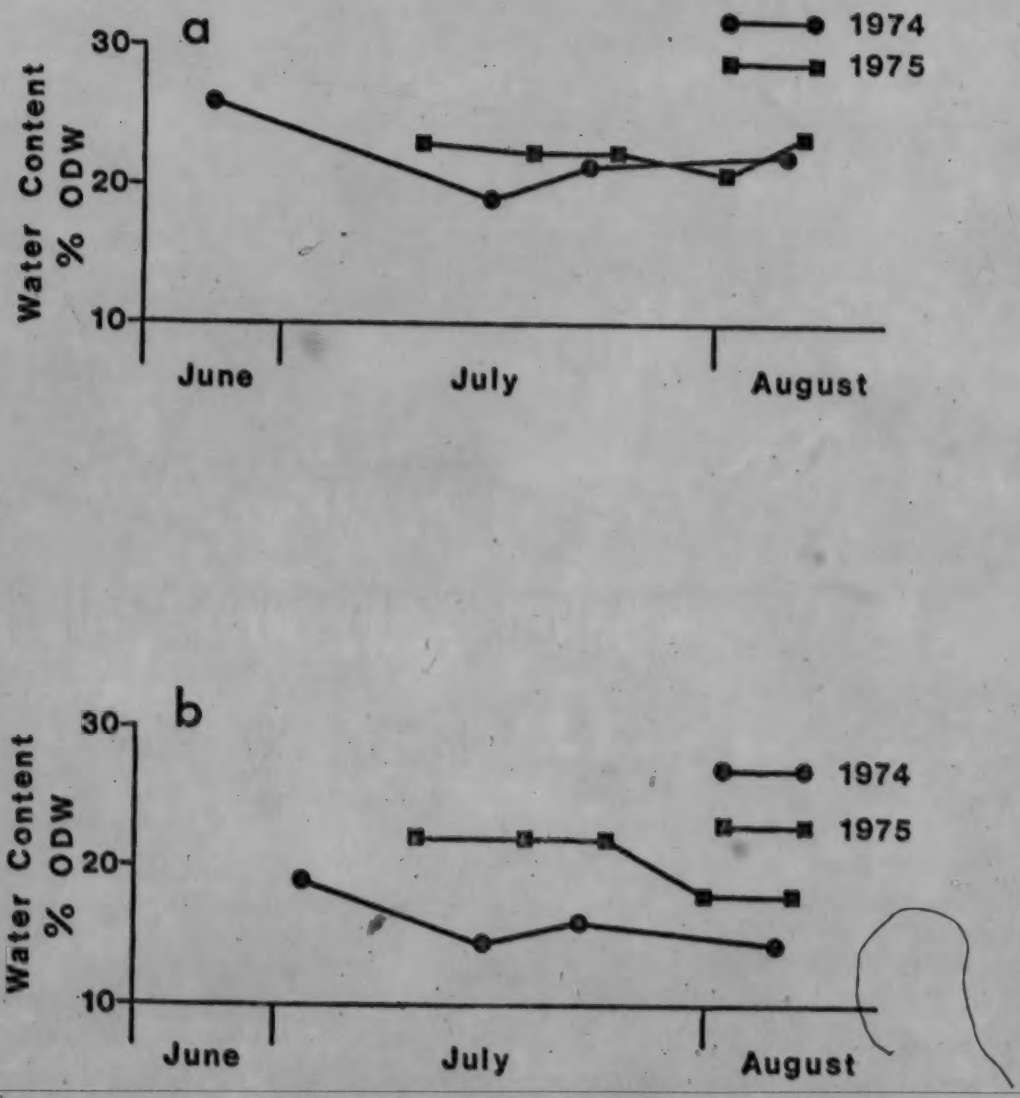

Figure 14. Soil moisture (0-5 cm) of the Moss-Lichen-Rush (a) and Lichen-Moss-Rush (b) communities during the summers of 1974 and 1975. Values are averages of 4 measurements.

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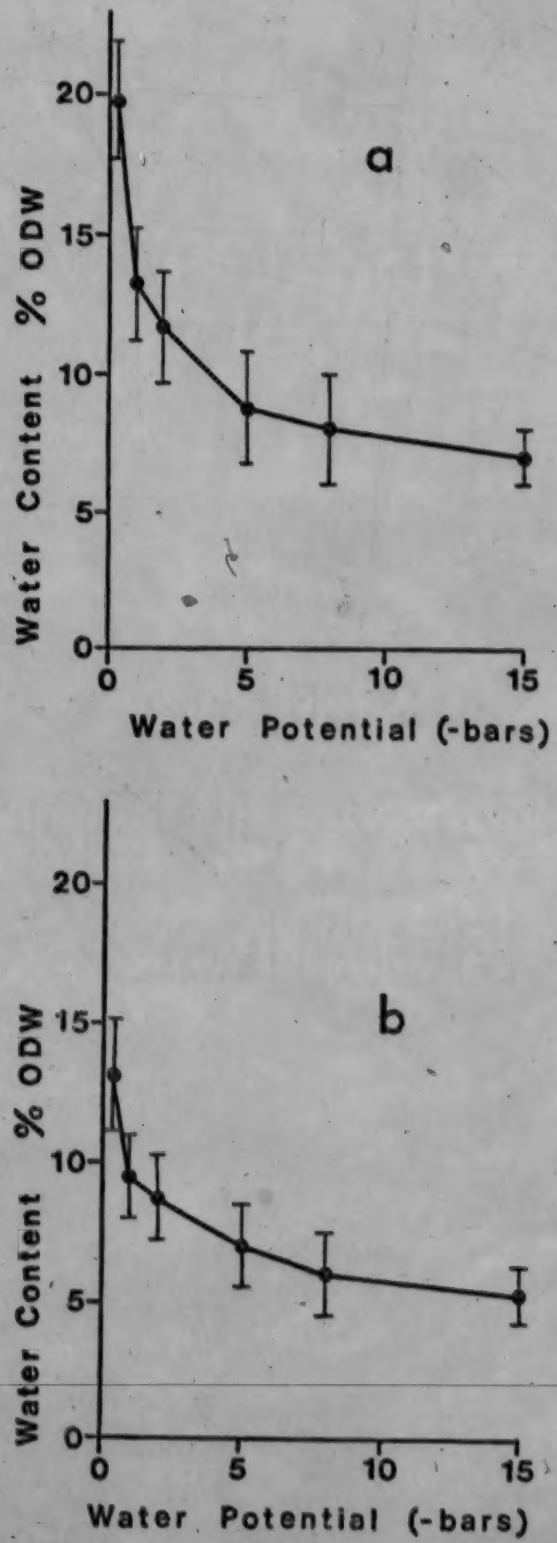

Figure 15. Water retention curves for soils (0-5 cm) from the Moss-Lichen-Rush (a) and Lichen-Moss-Rush (b) communities. Means ± 95% confidence limits.

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Although water content at the Lichen-Moss-Rush community was lower than that at the Moss-Lichen-Rush community, the values represent similar soil water potentials (Fig 15) and the sites had essentially identical water regimes from a biological point of view. The difference between water retention curves of the two soils resulted from differences in silt and clay fractions (Table 13) rather than differences in organic matter content (see Bell 1975). The Moss-Lichen-Rush soil had a higher percentage of silt and clay and hence, held more water than the Lichen-Moss-Rush soil at all pressures (Fig 15). There were no significant differences in either particle size distribution or water retention between sampling locations or between sampling depths and hence, all measurements at each site were clumped.

Table 13. Particle size of soils from two plant communities on King Christian Island. All values are in percent ± 95% confidence limits.

SITE	>2 mm	Sand 2-0.05 mm	Silt 0.05-0.002 mm	Clay <0.002 mm
Lichen-Moss-Rush	3.48±0.38	75.56±2.45	9.38±0.47	11.55±2.37
Moss-Lichen-Rush	1.34±0.11	69.16±0.90	15.18±1.30	14.32±1.67

CONCLUSIONS

As with all sections under the broad heading of Environment, the major conclusions must await presentation of plant physiological information and hence, only a few generalizations may be made here.

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The soils of Cape Abernathy area on King Christian Island were Regosolic Static Cryosols that had no morphological modification of the profile.

Soil moisture was above field capacity at both sites for most of the growing season indicating that water should not be a limiting factor for plant growth at either site.

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PLANT CHARACTERISTICS

INTRODUCTION

Luzula confusa is a circumpolar arctic-alpine rush that is both widespread and common throughout the North American Arctic. In the Canadian Arctic Archipelago, Luzula confusa occurs on almost all of the larger islands (Porsild 1955). The habitat of Luzula includes some of the most rigorous arctic environments, and the species appears to be among the hardiest and most typically high arctic of all plants (Polunin 1948). On King Christian Island, the greatest plant cover occurs in a narrow band about 1.5 Km wide, 1 Km from the coast. Luzula confusa was a major component of this vegetation (see Plant Communities p 10; Bell 1975).

METHODS AND MATERIALS

Observations of several characteristics that may aid in the survival of Luzula confusa were made both on King Christian Island and in the laboratory. Ten plants, approximately 15 cm in diameter, were collected on King Christian Island and examined in detail to estimate number of leaves produced, average age of tillers, plant age, and structure of above- and belowground components. The speed of growth initiation in the spring was determined by comparing the average length of green

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material (cm) with the average depth of the active layer (cm) for approximately 60 plants during snow-melt.

Five cores (28 cm^2 X 15 cm deep) were taken at the peak of the growing season (early August) to determine the various biomass components of the plant (standing dead, aboveground live, rhizomes, and roots at several depths). Cores were divided into 6 parts at depths of +4, +2, 0, -1, -5, -10 and -15 cm. Most divisions were based on plant characteristics: +4 cm represented the top of the vegetative canopy; +2 cm, top of the moss layer; 0 cm, moss-mineral soil interface and -1 cm, maximum penetration of rhizomes. Other divisions at -5, -10 and -15 cm were arbitrary and coincided with the positions of soil moisture and temperature measurements.

RESULTS AND DISCUSSION

GROWTH FORM

Most Luzula confusa plants in the Polar Semi-desert area of King Christian Island were 15 to 30 cm in diameter and approximately 4 cm high. Moss grew between the tillers and formed a mat about 2 cm thick. The resultant growth form was tufted and extended only slightly above the surface. Since temperatures are higher near the soil surface (see Climatology and Microclimatology p 34), and since arctic plant growth appears to be limited mainly by low summer temperatures (Billings 1974, Tieszen 1972), the growth form of Luzula may be an important plant characteristic permitting

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survival and growth in the King Christian Island environment. The importance of a low growth form, tightly apressed to the soil surface has been described in detail in relation to arctic and alpine cushion plant survival (Heilborn 1925, Spomer 1964, Bliss 1971, Corbet 1972, Addison 1976). The persistence of dead leaves in their upright position may also be of importance in improving the thermal regime. These leaves act as a windbreak, increasing the zero plane displacement, decreasing convective heat flux and resulting in higher leaf temperatures. The tufted nature of Luzula may also be important in trapping snow and hence, providing greater winter protection and more moisture in the spring.

AGE

Individual tillers of Luzula produced 14.5 ± 1.3 (mean ± 95% confidence limits) leaves during their life span. Each tiller had 4 leaves present during the growing season but since each leaf lived for 2 years, yearly leaf production was 2 leaves per tiller. This estimate is identical to leaf production of Luzula nivalis on King Christian Island (Bell 1975) and of Luzula confusa on Greenland (Sørenson 1941). Assuming that two leaves were produced yearly, the average life span of a tiller was about 7 years. This corresponds closely with age estimates of Luzula confusa tillers on Greenland (Sørenson 1941).

The age of entire plants was estimated in two ways. On a rhizome, initiation of a new tiller occurred when the

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youngest tiller was approximately 3 to 4 years old. Since the life expectancy of a tiller was about 7 years, two tillers were alive at all times if no premature death occurred. On the plants examined, only 25% of the tillers were alive and plant age was calculated from Equation 6.

$$AGE = \frac{\text{Total tillers}}{\text{Live tillers}/2} \times RT \qquad (6)$$

where RT is the replacement time (ca. 3.5 years). This resulted in an estimated plant age of about 30 years. Rhizome branching however, results in an underestimate of age both because of the potential time lag involved in branching and the increase in the ratio of living to total tillers. A rhizome that has two branches will have 4 rather than 2 tillers alive at any one time. Since rhizome branching occurred frequently, 30 years must be considered as the minimum possible age of the plants examined.

Plant age was also estimated by multiplying the number of tillers in a row along the longest rhizome branch by the replacement time (ca. 3.5 years). The average number of tillers in a row was 32.3 ± 5.6 which resulted in plant age estimates from 94 to 132 years. It is felt that this latter estimate was more realistic and that the plants used for both field and laboratory experiments were approximately 110 years of age. Plant age is an important factor when the long-term effects of environmental factors are considered.

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REPRODUCTION

Sexual reproduction of Luzula confusa on King Christian Island appears to be limited by the physical environment and, in fact, no viable seed was produced during the three years of study (Bell 1975). The plant relies heavily on vegetative reproduction and new tillers are produced every 3 to 4 years. It is not until the seventh year that a tiller flowers and dies. Even flowering may have a greater impact on vegetative reproduction than on sexual reproduction since rhizome branching appears to occur either more frequently or exclusively at the point of attachment of flowering tillers. The shift from leaf to floral meristem may reduce apical dominance and permit growth of lateral buds on the rhizome. Rhizome branching however, does not occur with each flowering. The observations of Luzula support the generalization that under environmental stress, sexual reproduction is less important than asexual reproduction (Bliss 1971, Savile 1972).

Luzula confusa seeds did not mature fully in any of the three study years (Bell 1975). It is expected that mature seeds may be dormant owing to an inhibitor in the seed coat (Bell 1975) similar to that reported for L. spicata and L. parviflora in the Alpine (Bell and Amen 1970). In general, seed dormancy is relatively rare in arctic and alpine species (Billings 1974) but it may be this dormancy that contributes to the success of the species that possess this characteristic (Amen 1966, Bliss 1971, Billings 1974).

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Seedling establishment in arctic and alpine areas appears to be controlled mainly by temperature, growing season length and water availability (Billings 1974). Although no seedlings of Luzula were found, the position of the plant's rhizome gave an indication of how establishment may have occurred. Rhizomes were found along the interface between a moss layer and the mineral soil. This suggests that the moss was there before the plant invaded and may have acted as a seedbed for it. Otherwise, rhizomes would be below the surface of the mineral soil. In revegetation studies on King Christian Island, a moss substrate substantially decreased mortality of several native species (Addison and Bell 1976). Mosses therefore, appear to provide a much more suitable environment for seedling growth than mineral soil because they provide a substantial water supply, higher temperatures (see Energy Budgets p 58), winter protection from desiccation and mechanical abrasion and little resistance to the penetration of roots. In the rigorous environment of King Christian Island, a moss seedbed may be not only beneficial but essential to the survival of Luzula confusa seedlings and those of other vascular species.

GROWTH

Rapid growth initiation in spring is an important characteristic of arctic plants since it permits full

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utilization of the short growing season and enhances survival in the rigorous arctic environment (Bliss 1971, Savile 1972, Billings 1974, Tieszen and Wieland 1975). The perennial nature of Luzula confusa with its large rhizome and winter-green leaf bases, permits the plant to commence growth almost immediately upon snow-melt. Measurements of active layer depth and green leaf length in the spring indicated that leaf expansion commenced when the active layer was less than 6 cm thick. On King Christian Island, the soil thawed 4.9 $\pm$ 1.2 cm on the first day after snow-melt and it appears therefore, that Luzula required less than two snow-free days to commence growth. This speed of spring initiation compares closely with arctic graminoids at Barrow, Alaska (Tieszen 1972).

Luzula has a periodic growth pattern (Sørenson 1941) and on King Christian Island, leaves started to go dormant 45 to 50 days after the initiation of growth. Bell (1975) found that root growth of Luzula confusa dropped to almost zero between 6 and 7 weeks after snow-melt in 1974. It appears therefore, that fall colouration of leaves is a reasonable indication of whole-plant senescence. This contrasts with Carex stans in wet sedge-moss meadows (Devon Island) where root growth continued two weeks after leaf senescence (Muc 1976). Periodic growth provides insurance against winter injury but sacrifices the opportunity for extensive growth in a favourable season (Savile 1972).

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BIOMASS

Only 5.8% of the aboveground biomass of Luzula confusa was alive (Table 14) and hence, it was the standing dead material that gave the plant the characteristic tufted appearance. The adaptive significance of this growth form has been discussed previously (see Growth Form p 73). Although the aboveground biomass was separated into living and dead components, the belowground biomass was not (Table 14), and hence, it was not possible to determine the living root to shoot ratio of the plant directly. Two indirect estimates of root to shoot ratio were made: the first using total aboveground and belowground biomass and the second, by assuming that the living to dead ratio was the same both above and below ground. Luzula had an estimated belowground to aboveground ratio of 0.71 and an estimated live root to shoot ratio of 0.39. These estimates are quite close to live root to shoot ratios of 15 King Christian Island plant species (0.1 to 1.0; Bell 1975) and for several other Polar Semi-desert areas (0.2 to 0.7; Khodachek 1969, Aleksandrova 1970, Svoboda 1973). The low root to shoot ratios in Polar Semi-desert areas appears to result from a very hostile soil environment (Bliss et al. 1973, Bell 1975).

Most of the root biomass of Luzula (80%) was in the top 5 cm of the soil (Table 15) even though the active layer thawed to a depth of 45 cm. This is quite different from

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Table 14. Biomass components of Luzula confusa on King Christian Island (mean ± 95% confidence limits). Area is based on the cover of Luzula of the Lichen-Moss-Rush Community.

Component	Biomass g m^{-2}	% of Total
Aboveground Total	16.76 ± 9.52	58.4
Live	0.97 ± 0.81	3.4
Standing Dead	15.79 ± 8.95	55.0
Rhizomes	5.53 ± 2.98	19.3
Roots	6.42 ± 2.12	22.4
TOTAL	28.71	100.1

Table 15. Vertical distribution of roots of Luzula confusa on King Christian Island (mean ± 95% confidence limits). Area is based on the cover of Luzula at the Lichen-Moss-Rush Community.

Depth (cm)	Biomass g m^{-2}	% of Total
Moss	0.42 ± 0.32	6.6
0 - 1	1.81 ± 0.62	28.2
1 - 5	2.95 ± 1.62	44.9
5 - 10	0.96 ± 0.71	16.0
10 - 15	0.28 ± 0.26	4.3
TOTAL	6.42 ± 2.12	100.0

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many low arctic sites where some sedge and grass roots have been shown to penetrate to the permafrost table (Bliss 1956, Billings and Shaver 1972). Luzula roots appear to be concentrated in the most favourable thermal environment in the soil; emphasizing the importance of temperature in this high arctic site. Having the bulk of the root system in the warmest soil environment would also enhance water uptake because of increased membrane permeability and nutrient availability as a result of higher decomposition rates. Bliss et al. (1973) indicated that low soil temperatures were more important than permafrost in reducing the extent of root penetration in the High Arctic. On King Christian Island, there were essentially no roots of Luzula below 15 cm.

No real comparison can be made of Luzula biomass with total vascular plant biomass of other Polar Semi-desert areas since the whole plant community was not sampled. Bliss and Svoboda (1977a) however, reported a live vascular plant biomass of 9 g m^{-2} in an adjacent area on King Christian Island. This value is the lowest live biomass estimate from any Polar Desert or Polar Semi-desert area reported (Bliss and Svoboda 1977b). The community sampled by Bliss and Svoboda (1977a) and the Lichen-Moss-Rush community appeared to have similar standing crops (visually). Assuming this, Luzula confusa accounted for 15% of the live vascular plant biomass while covering only 1.4% of the area. It appears therefore, that on the basis of biomass, Luzula confusa is much more important than its cover would indicate.

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WATER RELATIONS

INTRODUCTION

Most of the Arctic receives less than 250mm of precipitation annually, and since most falls as snow during the period when plants are not active (Thompson 1967), water is potentially a critical factor in the survival of arctic plants. Late summer drought has been observed at several arctic sites where a deep active layer permits rapid surface drainage (Bliss 1956, Weller et al. 1972, Teeri 1973, Addison 1976). The role of water as related to arctic plant survival and functioning has been reviewed from both ecological (Bliss 1971, Billings 1974, Lewis and Callaghan 1974) and physiological (Courtin and Mayo 1975) viewpoints.

Water on King Christian Island did not appear to be a limiting factor for plant survival during any of the three years of this study (see Energy Budget p 59) but since many individuals of Luzula confusa had estimated ages of about 110 years (Plant Characteristics p 74), they may have been exposed to a few exceptionally dry years. Drought, therefore, could be of critical importance in the survival of the species in this area.

The aims of this portion of the study were 1) to quantify the water regime of the soil-plant-atmosphere continuum in the

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field and 2) to estimate the capabilities of Luzula confusa to withstand water deficit.

METHODS AND MATERIALS

Field and laboratory water regime

Leaf water potential (Ψ_l) of Luzula was determined with a chamber psychrometer constructed after the design of Mayo (1974) and using a Wescor Psychrometric Microvoltmeter (Model MJ-55). Entire tillers of Luzula were collected in the field, sealed in aluminum envelopes and transported to the field laboratory where they were cut into 0.5 cm lengths and sealed in chamber psychrometers. Less than 5 min elapsed between the collection of tissue and insertion into the psychrometers. The chambers were placed in a water bath to prevent the establishment of thermal gradients in the psychrometer body, and Ψ was measured with the Wescor meter after a 2 hr equilibration time. The equilibration time was determined experimentally by measuring Ψ of 20 tissue samples every 15 min until there was less than a 10% increase in Ψ per hour. Psychrometers were calibrated monthly with KCl solutions of known osmotic potentials. In all cases, the tillers used for water potential measurements were collected from the centre of the plant. This position was selected both to standardize technique and to obtain a representative Ψ_l value for the clump as a whole. The water potential of a

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central tiller was usually within 1 bar of the average of tillers at the 4 cardinal points (i.e. N, S, E and W) and was always within the range given by the 95% confidence limits (Table 16).

Table 16. Leaf water potential(bars) from various parts of a Luzula plant during a day with moderately high insolation (July 28, 1974).

TIME hr	CLUMP POSITION N	S	E	W	MEAN ± 95% cl.	CENTRAL TILLER
0400	-3.2	-3.6	-0.1	-3.2	-2.5 ± 2.6	-3.2
0800	-2.6	-3.7	-3.7	-4.9	-3.7 ± 1.7	-4.7
1200	-1.8	-2.3	-3.6	-2.4	-2.5 ± 1.2	-3.1
1600	-0.8	-4.4	-8.4	-5.0	-4.6 ± 5.0	-4.7
2000	-1.8	-6.1	-2.7	-4.2	-3.7 ± 3.0	-6.3
0000	-2.3	-1.1	-0.9	-1.5	-1.4 ± 0.9	-1.1

Osmotic plus matric potential ($\psi_\pi + \psi_\tau$) was determined with chamber psychrometers after freezing the tissue to break the cell membranes and hence, reducing turgor to zero. In the field, liquid propane (-40°C) was used to freeze the tissue whereas in the laboratory, liquid nitrogen (-196°C) was used. Since both ψ_l and ($\psi_\pi + \psi_\tau$) were determined for each tissue sample, turgor potential (ψ_p) could be calculated from Equation 7.

$$\psi_p = \psi_l - (\psi_\pi + \psi_\tau) \qquad (7)$$

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Atmospheric humidity was measured with a hygrothermograph (See Microclimatology p 19) and the water flux from plant to atmosphere was monitored with sod blocks (see Energy Budgets p 49). Live Luzula leaves were harvested from the sod blocks when they were replaced every two weeks. The leaves were dried at 80°C for 24 hr. Leaf area was determined using a linear regression of area versus oven dry weight (leaf area in cm^2 = -4.0701 + 390.28 x oven weight in grams; r = 0.89). Leaf area for the regression was determined by the Ballotini glass bead technique (Thompson and Leyton 1971).

In the laboratory, Ψ_l, $(\Psi_\pi + \Psi_p)$ and Ψ_p were determined daily during a 48 day growing period. All plants used in laboratory experiments were collected in the field at the end of the growing season, potted with their native soil and given a "dormancy" period of more than 2 months at -5°C. After the dormancy period, the plants were grown under the conditions shown in Fig 16. Air temperature ranged from 0.03 cal cm^{-2} min^{-1} (0.0 μE m^{-2} sec^{-1} PAR) (night) to 0.24 cal cm^{-2} min^{-1} (540 μE m^{-2} sec^{-1} PAR (day). The light spectrum under various chamber light levels is presented in Appendix A.

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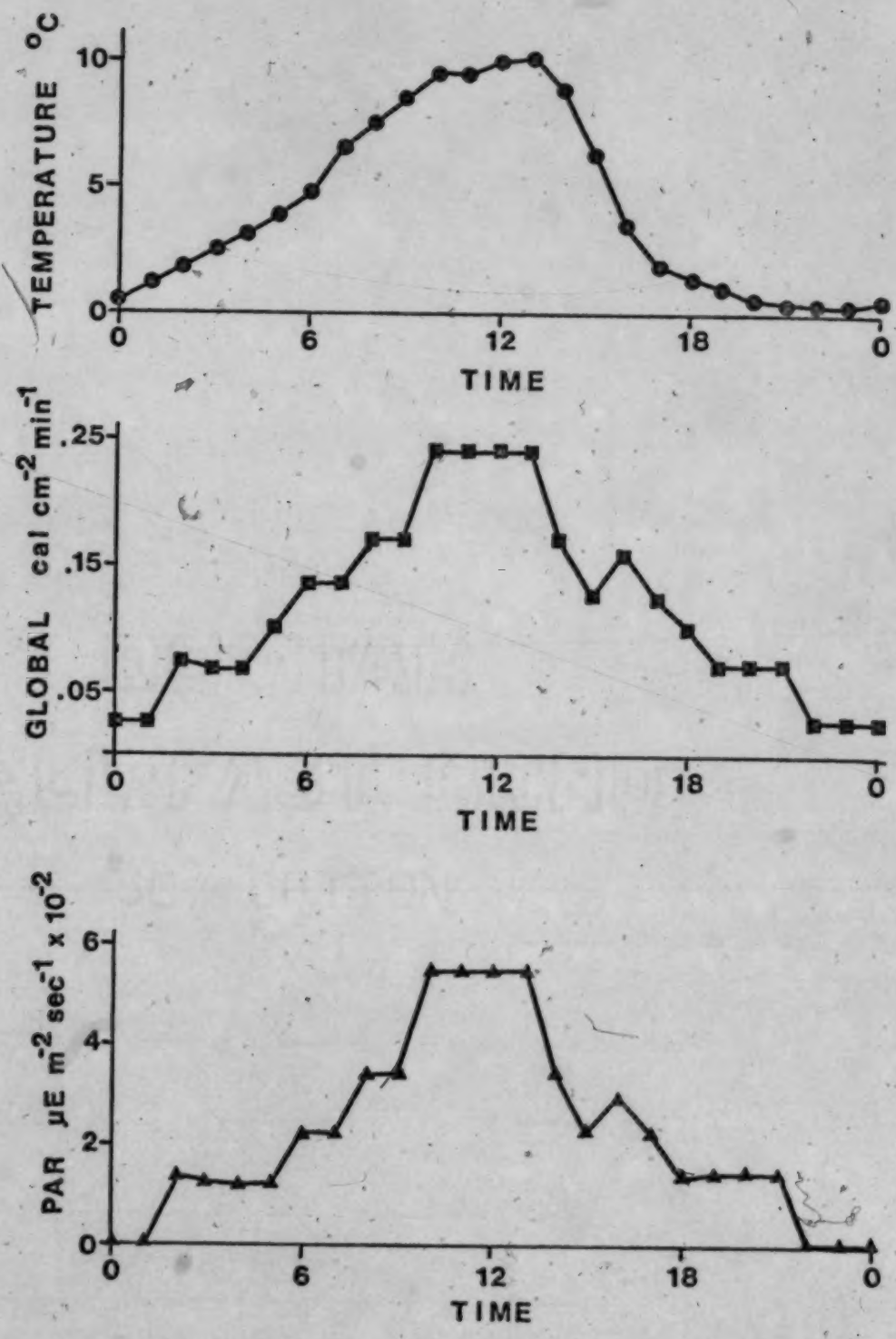

Figure 16. Growing conditions in the environmental growth chambers used for all plants involved in laboratory experiments.

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Physiological response to water deficit

The resistance that Luzula leaves imposed on water flux was calculated for periods when the plant showed signs of water deficit (i.e. $\Psi_p < 1$ bar) in order to estimate the capability of the plant to withstand drought. The total resistance of the water transfer pathway from leaf to air (Fig 17) was calculated from Equation 5 (p 59) and then the resistance owing to the laminar boundary layer of the leaves and the canopy was calculated and subtracted from the total.

The sum of boundary layer and canopy resistances was calculated by combining the heat transfer equation of Raschke (1960) with the ratio of the diffusivities of water vapour and heat in air (Slatyer 1967) into Equation 8.

$$r_a \doteq \frac{1.82\, c\rho(T_1 - T_a)}{H} \qquad (8)$$

where r_a is the resistance of the boundary layer and canopy to water vapour transfer (sec cm^{-1}); c, specific heat of air (cal $g^{-1}\ {}^{o}C^{-1}$); ρ, density of air (g cm^{-3}); T_1 and T_a, temperature (^{o}C) of leaf and air respectively, and H, sensible heat flux (cal $cm^{-2}\ sec^{-1}$) calculated from Equation 4. The assumption that sensible heat flux was equal from both leaf surfaces whereas water loss was from only the one surface that had stomata has also been incorporated into Equation 8. Because of the methods used, the possible error in r_a is extremely large (Appendix B).

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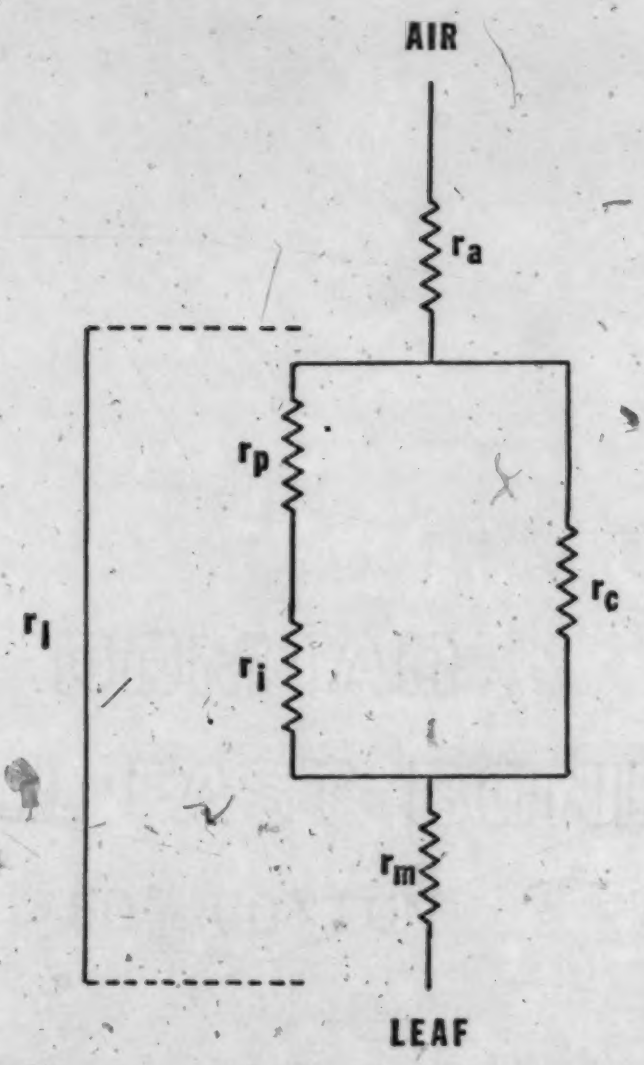

Figure 17. Diagramatic representation of the resistances to water vapour transfer from leaf to atmosphere.

r_a - boundary layer and canopy
r_l - leaf
r_i - intercellular space
r_p - stomatal
r_m - mesophyll
r_c - cuticle

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Since the resistance of the intercellular spaces (r_i), mesophyll (r_m) and cuticle (r_c) are usually relatively constant (Slatyer 1967), it follows that changes in leaf resistance (r_l) were caused by changes in stomatal aperature (r_p); the biological control of water loss.

The response of the stomata to decreasing water content is a function of the elasticity of the cell walls (Warren Wilson 1967), and in order to estimate this elasticity, the response of leaf water potential and its components to decreasing relative water content (RWC) was determined for entire Luzula tillers. Experiments were conducted under laboratory conditions at two plant phenological stages (i.e. preflowering and during die-back). Relative water content was calculated from Equation 9 (Slatyer 1967).

$$RWC = 100 \frac{(W_f - W_d)}{(W_t - W_d)} \qquad (9)$$

where W_f is the fresh weight; W_t, turgid weight, and W_d dry weight.

Entire plants were well watered and enclosed in plastic bags for 24 hr in order to maximize both Ψ_l and RWC. It was assumed that all tillers of one plant enclosed for the 24 hr period had the same RWC and Ψ_l. The relative water content of the plant as a whole was estimated by measuring RWC of 4

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entire, non-flowering tillers. These tillers were weighed (W_f), floated on distilled water for 4 hr and reweighed (W_t) before they were dried at 80°C for 24 hr (W_d). Other tillers from the same plant were detached, weighed and allowed to lose known amounts of water before being transferred to chamber psychrometers. Water loss from detached tillers was necessary to provide a range of RWC, ψ_l, $\psi_\pi + \psi_\gamma$ and ψ_p. Water potential, its components and oven dry weight were determined as described above. Relative water content was calculated from Equation 9 and making the correction in W_t based on the amount of water per gram (W_d) that the tillers floated on water had absorbed. The average RWC obtained after sealing the entire plant for 24 hr was greater than 95% in all cases.

The coefficient of expansion of Luzula cell walls (Y) was calculated from Equation 10 (Warren Wilson 1965).

$$Y = (\psi_\pi^\circ + \psi_\gamma^\circ) - \frac{(\psi_\pi^\circ + \psi_\gamma^\circ) + \psi_p^i}{1 - RWC_i} \qquad (10)$$

where $(\psi_\pi^\circ + \psi_\gamma^\circ)$ is the sum of osmotic and matric potentials at full turgor (i.e. RWC = 100%); RWC_i, some relative water content less than full turgor (arbitrarily taken at 90% and ψ_p^i, turgor potential at RWC_i.

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RESULTS AND DISCUSSION

Field and laboratory water regime

Seasonal

Water content of the top 5 cm of the soil was above field capacity (-1/3 bar) for most of the 1974 summer season (see Soils p 67). In general, the soil represented an adequate available water supply that was comparable to the wet meadows at Barrow, Alaska (Stoner and Miller 1975) and Devon Island, N.W.T. (Addison 1976).

Leaf water potential (Fig 18A) was low (i.e. -10 bars) in early July, 1974 but increased over a 10 day period to about -5 bars where it remained for most of the growing season. High atmospheric humidity appeared to be responsible for the low transpiration rates that permitted a shallow soil to leaf water potential difference (2.3 bars). Mean seasonal vapour pressure deficit (< 0.5 mb) was less than is considered typical of either arctic (6-8 mb; Lewis and Callaghan 1974) or alpine (8-10 mb; Bell 1973) areas. The lower spring values appear to result from low soil temperatures (1-2°C) reducing root water uptake rather than dry air increasing water flux from leaves since atmospheric humidity was high throughout the season (see Climatology and Mirco-climatology p 28).

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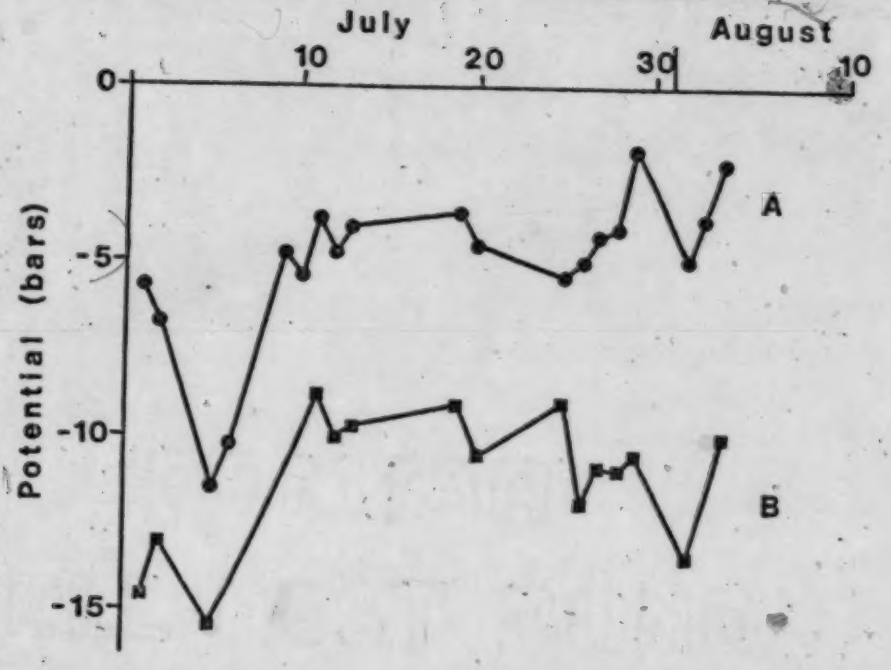

Figure 18. Leaf water potential (a) and osmotic plus matric potential (b) of Luzula confusa during the summer of 1974

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The seasonal pattern of leaf osmotic plus matric potential (Fig 18B) followed that of Ψ_l, and turgor potential (the difference between curves A and B in Fig 18) remained fairly constant at approximately 6 bars.

In the laboratory, when plants were watered on a regular basis (i.e. every 3 days), leaf water potential of Luzula was approximately -4 bars for most of the growing period. The lower Ψ_l and $(\Psi_\pi + \Psi_p)$ values recorded in the spring in the field (Fig 18), did not occur in the laboratory (Fig 19). This indicates that it was the field environmental conditions, rather than a characteristic of the plant during elongation, that was responsible for the depressed field values. Under both field and laboratory conditions, $(\Psi_\pi + \Psi_p)$ values decreased after the onset of die-back (on July 26; Fig 18 and Day 41; Fig 19). It is thought that this depression resulted from a higher proportion of the cell constituents becoming soluble for translocation in preparation for dormancy.

Daily

On a daily basis, Luzula exhibited severe water deficit (i.e. $\Psi_p < 1$ bar) on only one occasion (July 27, 1974) during the three years studied. Incoming radiation on this day reached the highest value recorded (1.15 cal cm^{-2} min^{-1}) and the 5 previous days had been free of either precipitation or fog (Fig 11, p 46).

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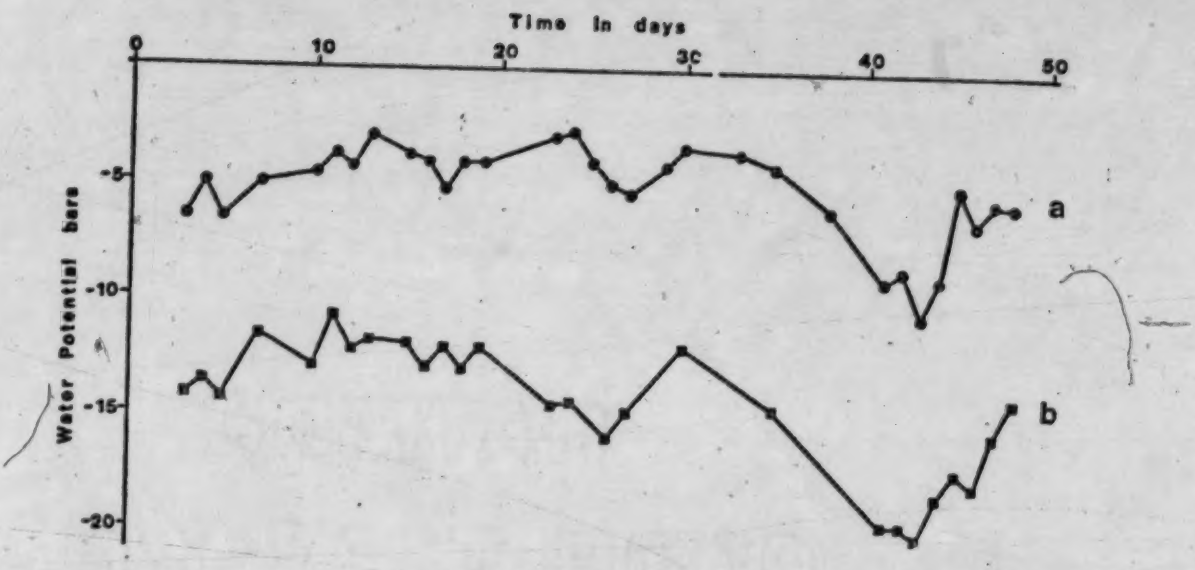

Figure 19. Leaf water potential (a) and osmotic plus matric potential (b) of Luzula confusa during a growing period in the laboratory. Values are averages of 4 readings taken between 08 and 10 h daily.

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In the early morning (0400 hr), transpiration started to increase (Fig 20C) in response to increasing radiant heat load on the surface, but at 0800 hr, there was a dramatic reduction in the rate. This decrease in transpiration could not be related to leaf temperature, air humidity or the radiant heat load. It appears that transpiration exceeded water uptake by the roots resulting in increased leaf water deficit and stomatal closure. Water and turgor potentials (Figs 20A and 20B respectively) were both low at the same time. Leaf resistance (Fig 20D) increased substantially indicating a dramatic reduction in stomatal aperature. The drop in turgor, Ψ, and transpiration appears to stem from the inability of the plant to draw water from cold soils. Soil temperature (-5 cm) at 0800 hr was only 4°C but had increased to 10°C by 1200 hr. A second reduction in leaf water potential, turgor and transpiration accompanied by an increase in leaf resistance occurred at 1200 hr. This second reduction appears to be more related to the steep vapour pressure gradient from leaf to atmosphere that caused the increase in water deficit in the leaf tissue. Vapour pressure gradient from leaf to atmosphere had increased from 3.0 mb at 0800 hr to 6.4 mb at 1200 hr. The second reduction in transpiration appears to be comparable to the "mid-day depression" of

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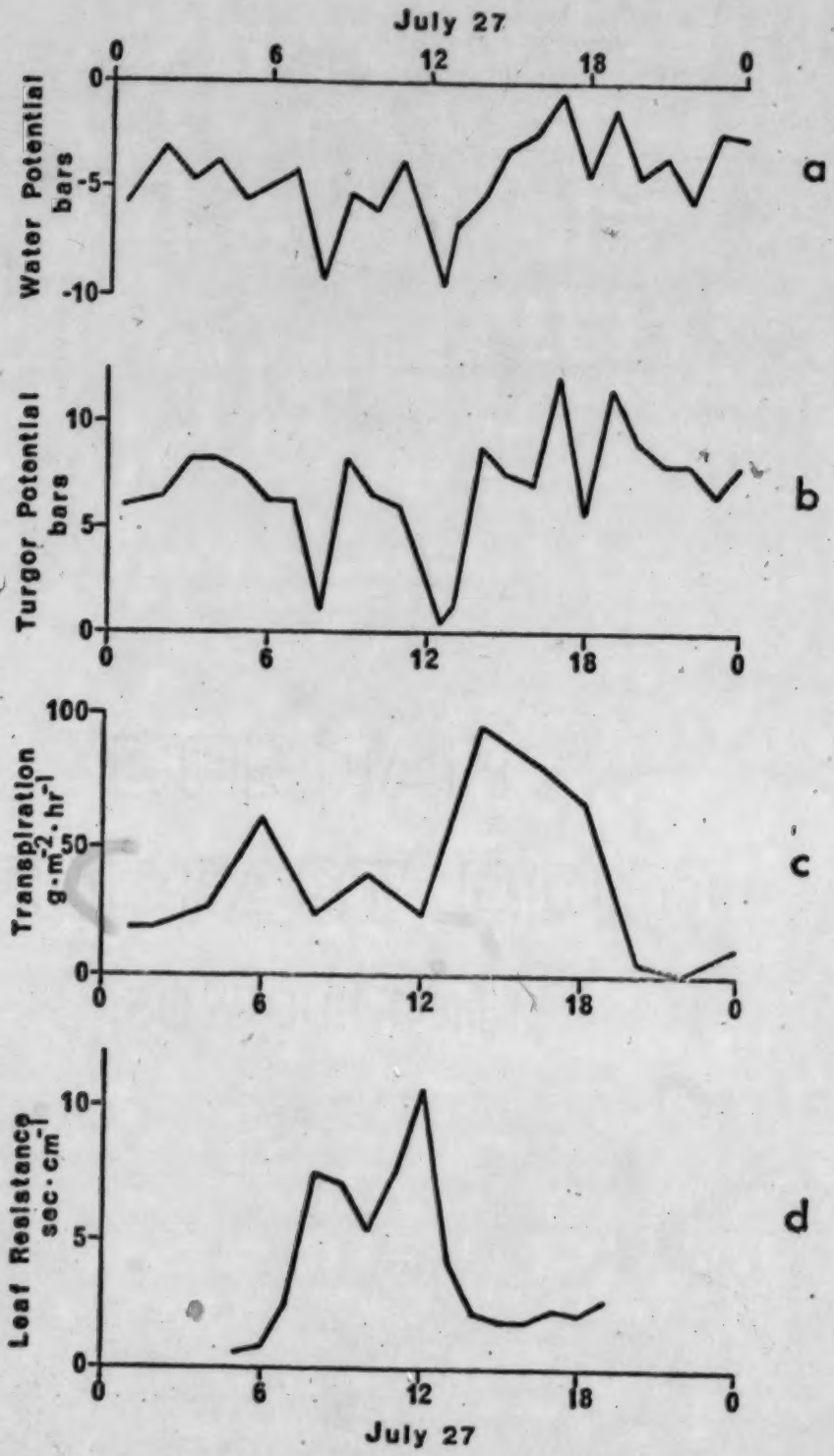

Figure 20. Leaf water potential (a), turgor potential (b), transpiration (leaf area basis) (c), and leaf resistance to water flux (d) of Luzula confusa during July 27, 1974.

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transpiration reported by Gates (1965) for mesophytic plants and Courtin (1968) for alpine species.

On August 2, 1974, when incoming radiation was moderately high (0.95 cal cm^{-2} min^{-1} at solar noon), Luzula did not appear to be limited by water at any time during the day. Leaf water potential (Fig 21A) did not drop below -10 bars at any time during the measurement period, and the minimum turgor potential reached was approximately 2.5 bars (Fig 21B). There was however, a reduction in transpiration rate at 1400 hr (Fig 21C) but this appears to be more influenced by changes in environmental conditions than an increase in leaf resistance (Fig 21D, Table 17). Leaf resistance did increase when transpiration decreased, but this is probably an artifact in the data since calculations of leaf resistance are highly dependent upon transpiration measurements (see Equation 5). The maximum leaf resistance of Luzula during August 2-3 was substantially less than on July 27 when water and turgor potential measurements indicated that the plant was experiencing severe water deficit.

On days with substantial cloud cover, water and turgor potentials were consistent and high while transpiration was low. On such days, leaf resistance was normally less than 2 sec cm^{-1} throughout the day.

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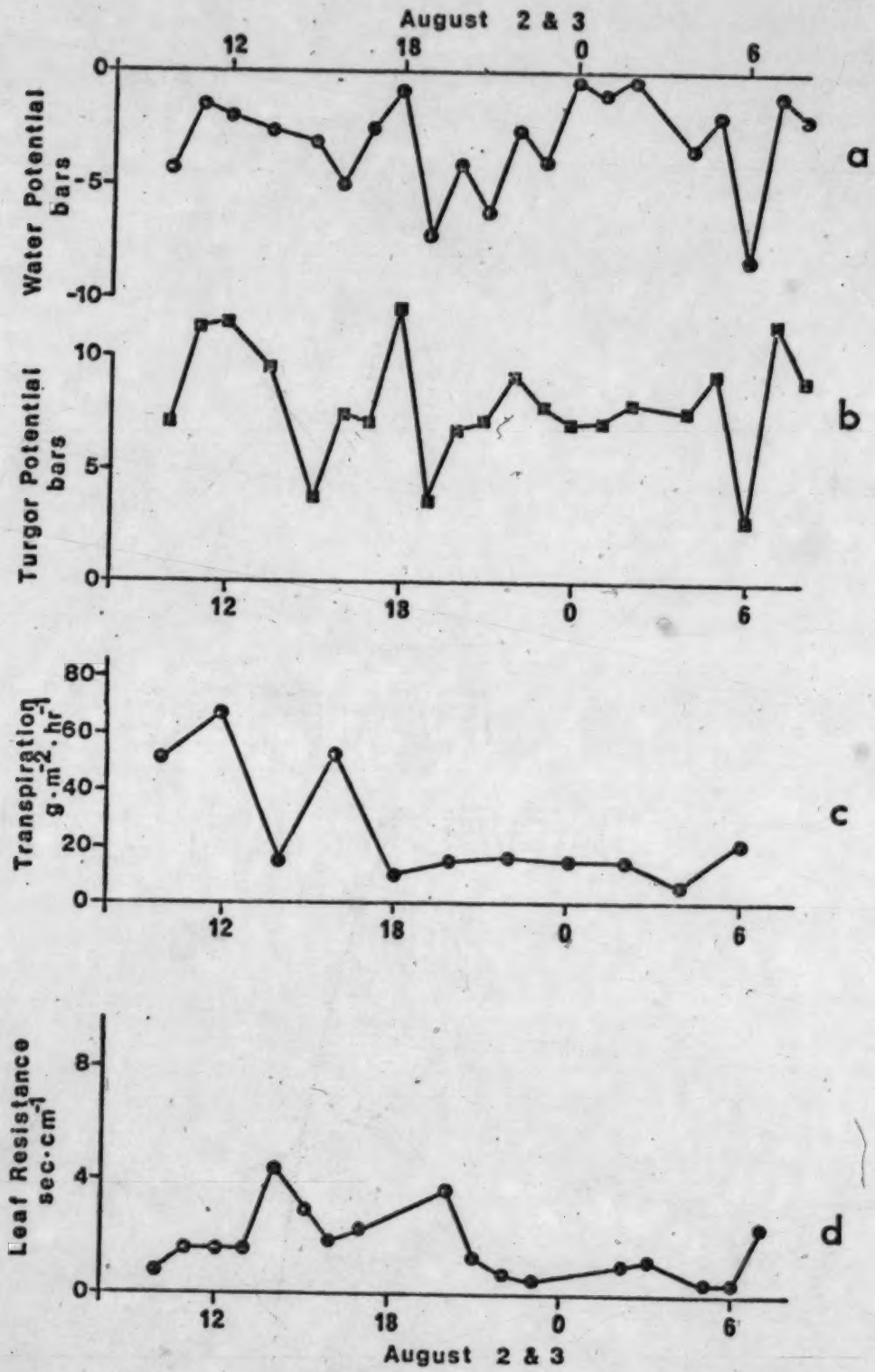

Figure 21. Leaf water potential (a), turgor potential (b), transpiration (leaf area basis) (c), and leaf resistance to water flux (d) of Luzula confusa during August 2 and 3, 1974.

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Table 17. Environmental conditions and plant response during a reduction in transpiration on August 2, 1974.

FACTOR	TIME 1200	1400	1600
Incoming radiation (cal cm^{-2} min^{-1})	0.95	0.87	1.00
Net Radiation (cal cm^{-2} min^{-1})	0.40	0.32	0.43
Leaf Temperature °C	10.6	7.8	9.6
Air Temperature °C	5.0	3.7	4.9
Vapour Pressure Gradient (leaf to air) (mb)	4.4	2.6	4.1
Transpiration (g m^{-2} hr^{-1})	66	15	53
Leaf Resistance (sec cm^{-1})	1.6	4.5	1.9

The minimum leaf resistance of Luzula calculated from the energy budget components (0.5-1.0 sec cm^{-1}) was comparable with that of plants growing in moist environments in both alpine (0.6 - 1.4 sec cm^{-1}; Ehleringer and Miller 1975) and arctic (1 - 3 sec cm^{-1}; Stoner and Miller 1975) areas.

Physiological response to water deficit

Laboratory studies on the response of Luzula to water deficit showed a shift with phenological stage (Fig 22). For all water potentials, the plant maintained a greater amount of water in its tissue late in the season (Fig 22B) than in the early part (Fig 22A). There was also a significantly

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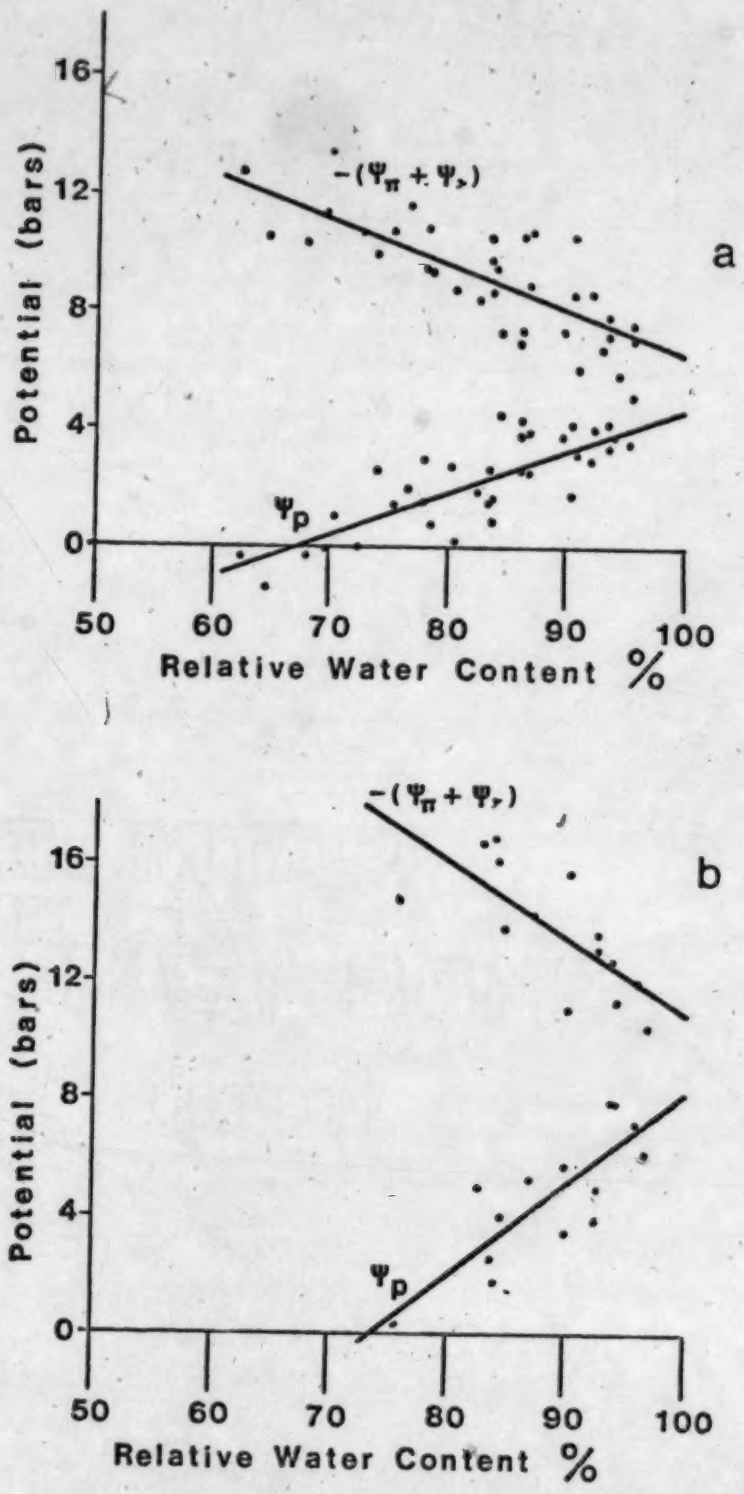

Figure 22. Osmotic plus matric potential ($\Psi_\pi + \Psi_s$) and turgor potential (Ψ_p) versus relative water content at the beginning (a) and end (b) of a laboratory growing period.

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greater reduction in turgor with decreasing relative water content in plants at the end of the growing season than those at the beginning (F_s test of regression lines p 0.05; Sokal and Rohlf 1969). This appears to be a mechanism that allows the plant to survive late season droughts and maintain sufficient water in its tissue to allow translocation of materials out of the leaf as it begins senescence. There was also a significantly greater reduction in $\psi_\pi + \psi_p$ with decreasing relative water content at the end versus beginning of the growing season. This is likely a response to senescence (greater soluble material present) and results in the maintenance of higher water content (osmoregulation).

The difference in cell wall properties (elasticity) between the two phenological stages (28 bar $\%RWC^{-1}$ early versus 48 bar $\%RWC^{-1}$ late) also indicates that the plants had a more sensitive control of water content at the end of the season than at the beginning. Both values of elasticity fall within the range of elasticities for arctic graminoids at Barrow, Alaska (recalculated from Johnson and Caldwell 1976).

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CONCLUSIONS

Water did not appear to be a limiting factor for plant survival on King Christian Island during the summers of 1973-75. This was probably because of high atmospheric humidity (VPD < 0.5 mb) that maintained a low transpiration rate and permitted a very shallow soil to leaf water potential gradient (2.3 bars) to be adequate to supply the plant with water. The average leaf water potential of Luzula was -5 bars and there were about 6 bars of turgor.

On the rare occasions when leaf water deficit was critical, (i.e. $\Psi_l < 1$ bar), transpiration rates were greatly reduced owing to the increase in leaf resistance from the normal 1 sec cm^{-1} to 8 - 11 sec cm^{-1}. On only one day did the leaf resistance reach this level.

Luzula appeared to be better able to resist water deficit at the end of the growing season than at the beginning, owing to the lower elasticity of the cell walls that resulted in a more sensitive control of water flux.

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PHOTOSYNTHESIS AND RESPIRATION

INTRODUCTION

The way in which arctic plants are physiologically adapted to and controlled by the environment has been under discussion for some time (Bliss 1962, Warren Wilson 1966, Billings and Mooney 1968, Bliss 1971, Savile 1972), but it has only been recently that *in situ* measurements of photosynthesis and resipiration in arctic regions have been possible (Shvetsova and Voznessenskii 1971, Mayo *et al.* 1973, 1976, Tieszen 1973). It has only been this recent field work that has permitted the testing of the many ideas derived in the laboratory.

In this study, net photosynthesis was used as an indication of plant metabolism in order to evaluate the influence of extrinsic (environmental) and intrinsic (phenological) factors on plant growth and survival. The specific aims of this portion of the work were: 1) to determine the influence of temperature, light and soil drying on net photosynthetic rate of *Luzula confusa* and 2) to determine what influence plant factors such as leaf age or phenological stage have on net photosynthesis.

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METHODS AND MATERIALS

Field Studies

Net assimilation rate (NAR), the difference between plant photosynthesis and respiration, was determined under field conditions. Individual tillers of Luzula were enclosed in cylindrical cuvettes (Plate 6) that were part of an open cuvette-gas analysis system (Šesták et al. 1971). The design of the gas flow system followed those of van Zinderen Bakker (1974) and Hartgerink (1975); Fig 23). Two cuvettes were used on a time sharing basis and carbon dioxide flux from air to plant was measured differentially with a Beckman Model 865 Infra-red Gas Analyser (IRGA). The output of the IRGA was recorded on a 26-channel Honeywell Potentiometric Recorder and was proportional to the difference in CO_2 concentration of air passing through the cuvette and that which did not (Sample - Reference, Fig 23). Full scale on the recorder represented a difference of 50 ppm CO_2 between the sample and reference cells in the IRGA. Calibration was carried out every 8 hr using air from 2 cylinders with known CO_2 concentrations (Consumers Specialty Gas, Inc.). The concentration of CO_2 in the gas cylinders had been previously determined with the IRGA by comparison with the known output from a gas mixing system (Wosthoff, Inc.). Dark respiration within each cuvette was measured occasionally after light was excluded by an aluminum cover.

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Plate 6. Cuvettes used for single tillers of Luzula confusa in both field and laboratory gas exchange studies.

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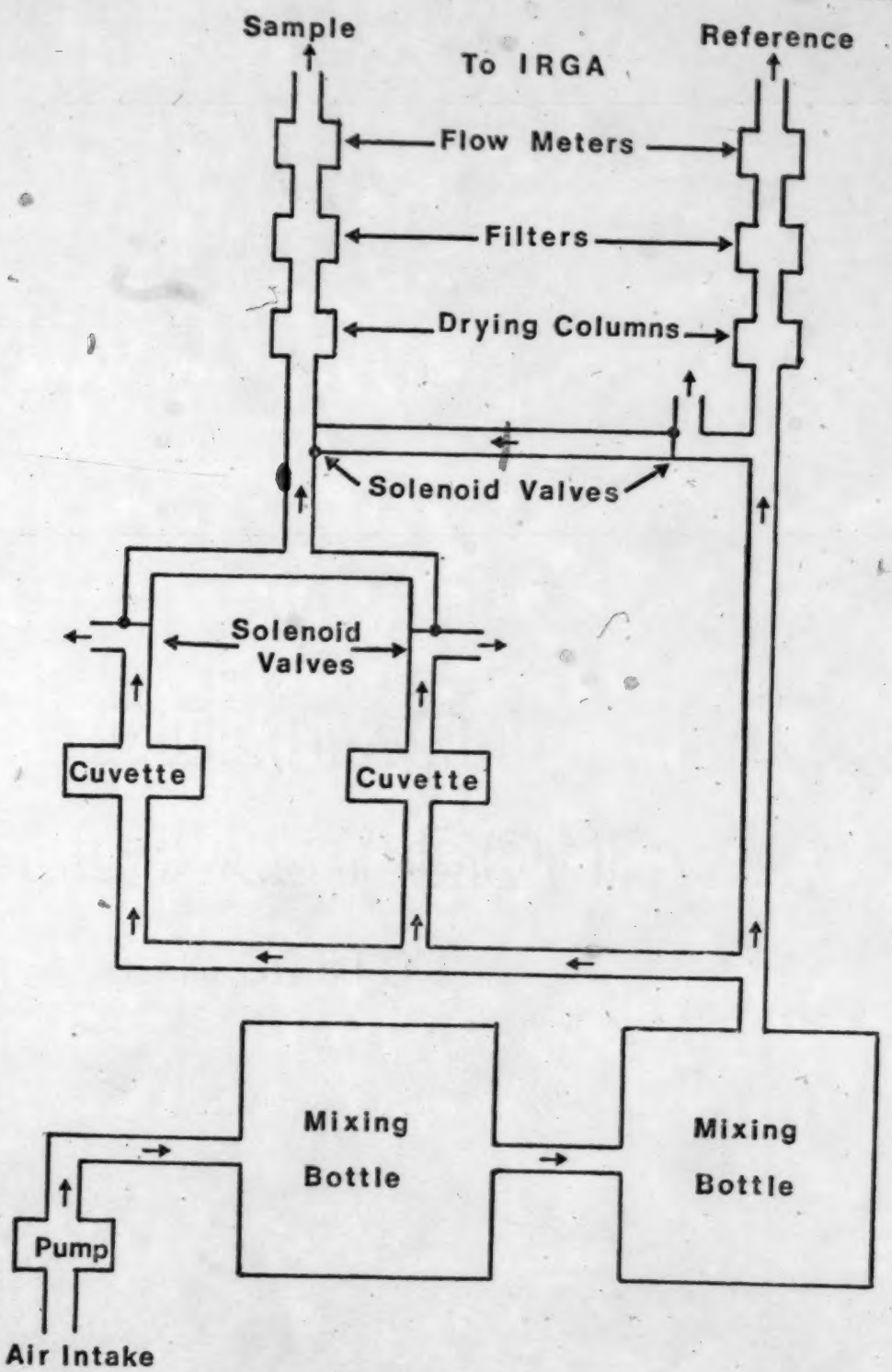

Figure 23. Open gas flow system used in both the field and laboratory.

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Power supply for the instrumentation was a 2500 W gas powered generator (Onan or Homelite) and the voltage and frequency were kept constant (110 VAC @ 60 Hz) by varying a "dummy" load of two 250 W light bulbs. The generator was kept downwind of the air intake of the air flow system at all times.

The instruments were housed in a heated tent and were insulated with plastic foam in order to maintain optimum operating temperatures.

Leaf and air temperature both inside and outside of the cuvette were monitored continuously with the recorder that was equipped with an electronic reference junction for copper-constantan thermocouples. Internal cuvette temperatures were kept as close as possible to ambient (0-5°C sunny and 0-2°C cloudy conditions) by adjusting the flow rate through the cuvette. Control of flow rate was accomplished by supplying the intake pump (Reciprotor, Inc.) with different voltages from a power transformer. Flow rates through each cuvette were typically between 50 and 150 ml min^{-1} depending upon both the heat load requiring dissipation and the rate of gas exchange by the plant.

Photosynthetically active radiation (PAR; 400-700 nm) was monitored continuously with a Lambda Quantum Sensor connected to the recorder. Components of the radiation

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regime were also monitored on the recorder using the sensors described above (see Climatology and Microclimatology p 19 and Energy Budgets p 49). Soil water potential and water content (see Soils p 66), leaf water potential and components (see Water Relations p 83), and evaporation and transpiration (see Energy Budgets p 49) were measured at regular intervals while net assimilation measurements were in progress.

At the end of the measurement period, enclosed tillers were harvested, dried at 80°C for 24 hr and weighed. Calculations of net assimilation rate (NAR in mg CO_2 g^{-1} hr^{-1}) were carried out following Equation 11.

$$NAR = \frac{\frac{Cuv - Amb}{S / C} * Z * \frac{T^{o}}{T_1} * F * 60.}{W_1} \qquad (11)$$

where Cuv is the scale reading on the recorder when the IRGA has air from the cuvette in the sample cell and ambient air in the reference cell; Amb, the scale reading when the IRGA has ambient air flowing through both cells; S, the difference in scale units between the IRGA reading when the same standard gas is flowing through both cells and that when each standard gas is flowing through one cell; C, the difference in CO_2 concentration between the two standard gases (ppm); Z, the conversion from ppm to mg CO_2 g^{-1} ml^{-1} ($44*10^{-6}/22.414$ mg CO_2 ml^{-1} ppm^{-1}); T^{o}, standard temperature (273.16 °K); T_1, leaf temperature (°K); F, flow rate (ml min^{-1}); 60., conversion from minutes to hours and, W_1, dry weight of the

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tiller (g). The potential error involved in the determination of absolute NAR measurements was approximately 15% mainly owing to possible errors in flow meter and standard gas concentration calibration. Reproducibility on the other hand, had a possible error of less than 6%.

Laboratory Studies

The same gas analysis system and cuvettes that were used in the field were also employed to determine net assimilation rates of Luzula under selected environmental conditions in the laboratory. All plants were grown under standard environmental conditions as described above (Water Relations p 83) and transferred to the "experimental" environmental growth chamber where light intensity and temperature could be manipulated. In all experiments, PAR and leaf and air temperatures were monitored. Air supply for the flow system was from the central air-conditioning system and two 10 l mixing bottles were employed in an attempt to obtain stable CO_2 levels in ambient air. In both laboratory and field studies, it was not possible to either control or measure atmospheric humidity in the cuvette with the instrumentation available.

Effect of Light and Temperature

Pairs of Luzula confusa plants, each with one tiller enclosed in a cuvette, were placed in the

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growth chamber where they were given a 2 hr period under each condition of light and temperature (Table 18). The sequence that the conditions were presented was selected in order to minimize after-effects of exposure to high or low temperatures on photosynthesis. An equilibration time of about 10 min was given before each reading and two measurements of each tiller were averaged to yield tiller NAR. Measurements of 10 to 15 tillers were taken under each pair of conditions.

Table 18. Order of temperature and light conditions during net assimilation studies.

LIGHT INTENSITY ($\mu E\ m^{-2}\ sec^{-1}$ PAR)	TEMPERATURE (°C)					
	0	5	10	15	20	25
0	34	4	8	12	16	20
150	31	1	5	9	13	17
350	32	2	6	10	14	18
550	33	3	7	11	15	19
900	**	21	23	25	27	29
1300	**	22	24	26	28	30

** Values not obtainable

The desired leaf temperature was achieved by adjusting both the temperature in the growth

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chamber and the flow rate through the cuvette. The lowest four light intensities were obtained by varying both the number of lights burning in the growth chamber (external controls) and distance between plant and light bank. For higher light intensities (i.e. 900 and 1300 μE m^{-2} sec^{-1}, PAR), growth chamber lights were supplemented by a 1000 W Tungsten-filament bulb complete with water jacket.

Effect of Drying

Four plants were grown for 20 days under standard conditions (see Water Relations p 83) and watered on a regular basis (every 3 days). At the end of this period, they were transferred to the growth chamber where they were given constant temperature and light conditions (10°C and 550 μE m^{-2} sec^{-1} PAR) and watering was stopped. Relative humidity in the chamber was about 60%. Net assimilation of one tiller from each plant was measured daily for 15 days. The same tiller was used throughout the drying period and was enclosed in the cuvette only for the time period required to measure NAR (i.e. 1 hr; 30 min equilibration and 30 min measurement). At the same time as NAR was measured, water potential and its components were also determined (see Water Relations p 83) for another tiller. It was assumed that all tillers of one plant had the same NAR and water potential.

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Effect of Phenology

Net assimilation rates of various non-flowering tillers from a single Luzula plant were measured continuously for a 24 hr period under standard conditions (see Water Relations p 83) at selected times during the growing period. The times represented four plant phenological stages including preflowering, anthesis, postflowering and dieback. The IRGA was calibrated both before and after the 24 hr measurement period and zero was checked hourly.

RESULTS AND DISCUSSION

Field Studies

Net assimilation of Luzula confusa on a day with moderate to high incoming radiation (July 24, 1975; Fig 24) appeared to follow both temperature and light intensity throughout the 24 hr arctic day. The generality that maximum net photosynthetic rates of arctic plants are obtained near solar noon and minima near solar midnight (Tieszen and Wieland 1974) appeared to hold, but CO_2 uptake was most strongly coupled to leaf temperature rather than light intensity as observed for other arctic plants (Tieszen 1973, Shvetsova and Voznessenskii 1971). During the "night" hours, Luzula often had positive net assimilation. The ability to show positive net photosynthesis throughout the 24 hr arctic

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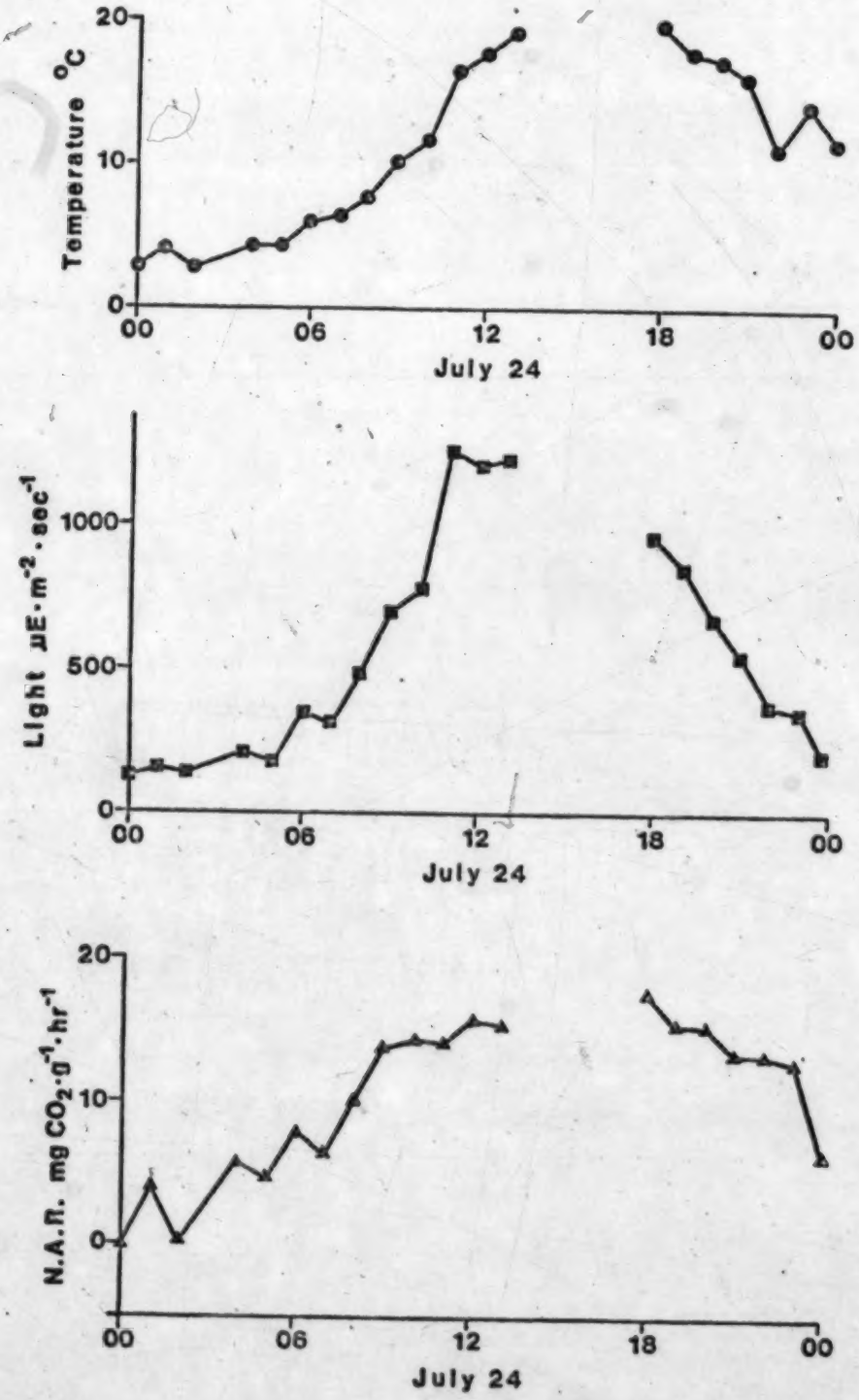

Figure 24. Net assimilation rate of Luzula confusa and environmental conditions during July 24, 1975.

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day appears to be a common characteristic of arctic plants (Mayo et al. 1973, 1976, Tieszen 1973) and Luzula confusa was no exception (Fig 24).

With the onset of dieback in the field, net assimilation rates dropped dramatically. Typical mid-day net photosynthetic rates ranged from 10 to 15 mg CO_2 $g^{-1}hr^{-1}$ during much of the growing period but dropped to between 2 and 5 mg CO_2 g^{-1} hr^{-1} with the onset of senescence. The reduction was not a result of increased respiration since there was also a slight drop in dark respiration (Table 19). The reductions in both net photosynthesis and dark respiration therefore appear to represent a general slowing down of plant metabolism with senescence.

Table 19. Net assimilation rate of Luzula confusa under selected environmental conditions before (July 28) and after (August 4) the onset of senescence. All values are averages of 3 samples.

DATE	LIGHT (μE m^{-2} sec^{-1})	TEMPERATURE ($^{\circ}C$)	NAR (mg CO_2 $g^{-1}hr^{-1}$)
July 28	274	3.7	4.37
	0	3.4	-2.32
Aug 4	335	3.5	1.17
	0	2.8	-1.31

Note: Negative values indicate respiration in the dark.

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Temperature appears to have the greatest effect of any environmental factor on the net assimilation rate of Luzula confusa. Using 60 hr of NAR measurements at the height of the growing season (July 23 to 26, 1975), it was found that there was a significant correlation between the logarithm (base 10) of leaf temperature (^{o}C) and NAR (mg CO_2 g^{-1} hr^{-1}) above a threshold temperature of 3 ^{o}C ($r = 0.93$; $p < 0.01$; Sokal and Rohlf 1969, p 509). A significant amount of the variability in NAR was accounted for by the regression of NAR on $\log_{10}$ temperature ($NAR = -9.1044 + 21.0152 (\log_{10} T)$; $p < 0.001$; Sokal and Rohlf 1969, p 420). Below 3 ^{o}C, NAR was not significantly correlated with leaf temperature. Since low leaf temperatures during the growing season are almost always associated with low light levels, it was expected that light might be limiting at these times. Light intensity (μE m^{-2} sec^{-1} PAR) was significantly correlated with NAR ($r = 0.96$; $p < 0.01$) below 3 ^{o}C and the linear regression of NAR on light intensity accounted for a significant amount of the variability in NAR ($NAR = -1.018 + 0.0119$ (light); $p < 0.001$). A more complete explanation of the field response is presented below (see Laboratory Studies; Effect of Light and Temperature p 124).

The influence of the field moisture regime on net assimilation rate was not explored. The ranges of soil and leaf water potentials were very narrow and it was not possible to observe any effect of moisture on NAR. In addition, a

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significant amount of the variability of NAR was accounted for by light and temperature alone.

An empirical model was constructed using the two regressions described above. The model used NAR regressed on log temperature above 3°C and NAR regressed on light below 3°C. A test of the model was carried out using NAR, leaf temperature and photosynthetically active radiation measurements from a day with moderately high incoming radiation (July 28, 1975). The data from this day were not used in the regression analyses. Although there were some differences between the predicted and the measured valued of NAR, especially at low light and temperature (Fig 25), the agreement was quite close and the model predicted a daily average NAR within 1 mg CO_2 g^{-1} hr^{-1} of the measured average (6.9 mg CO_2 g^{-1} hr^{-1}). Under cloudy conditions (Aug 1, 1975), the difference between predicted and measured net photosynthesis on a daily basis (1.3 vs. 0.9 mg CO_2 g^{-1} hr^{-1}) was also low.

Laboratory Studies

Effect of Light and Temperature

Light

Luzula confusa responded to increasing light intensity (Fig 26) like most C_3 plants (Hesketh and Moss 1963) and light saturation appears to occur well below full sunlight

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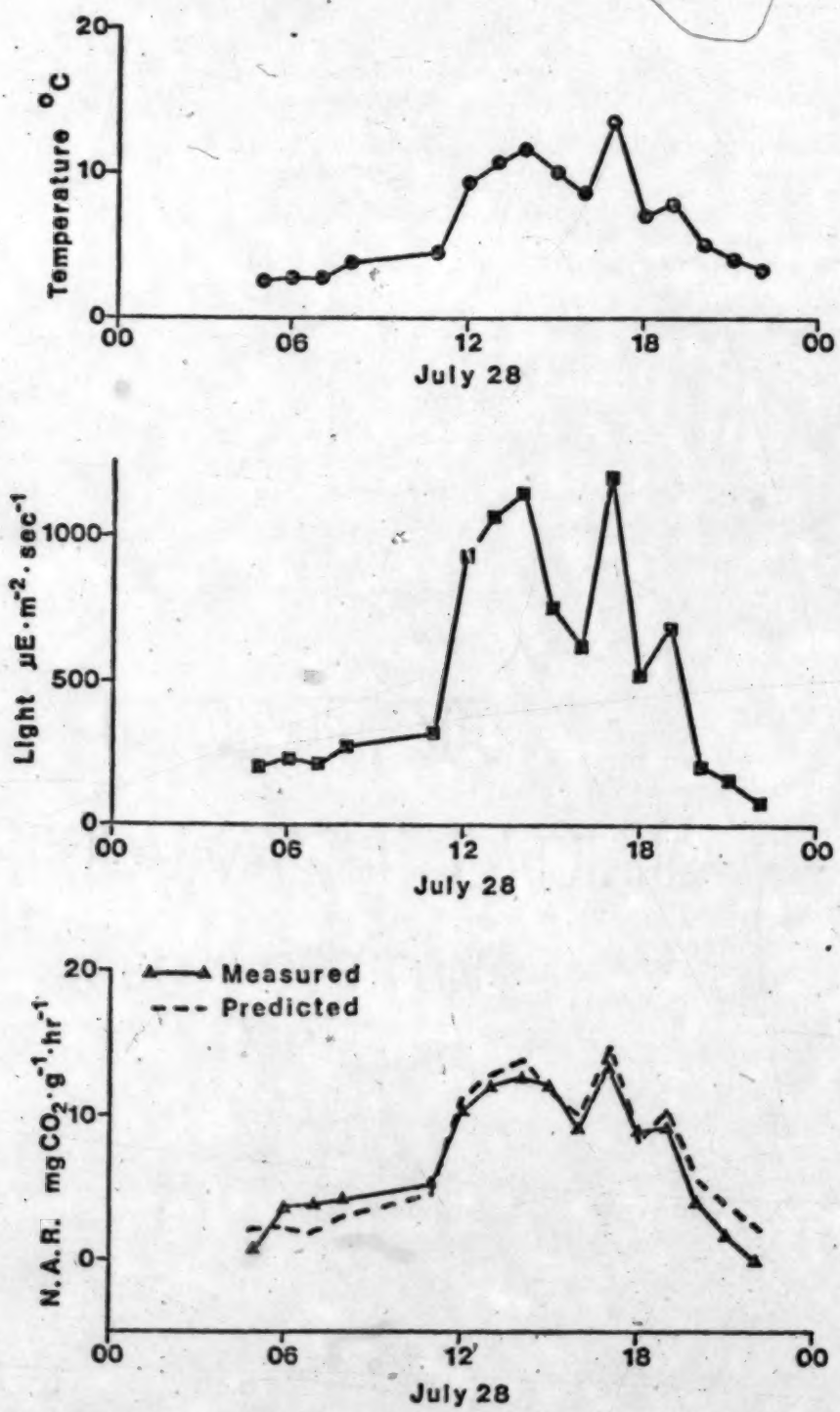

Figure 25. Net assimilation rate of Luzula confusa and environmental conditions during July 28, 1975.

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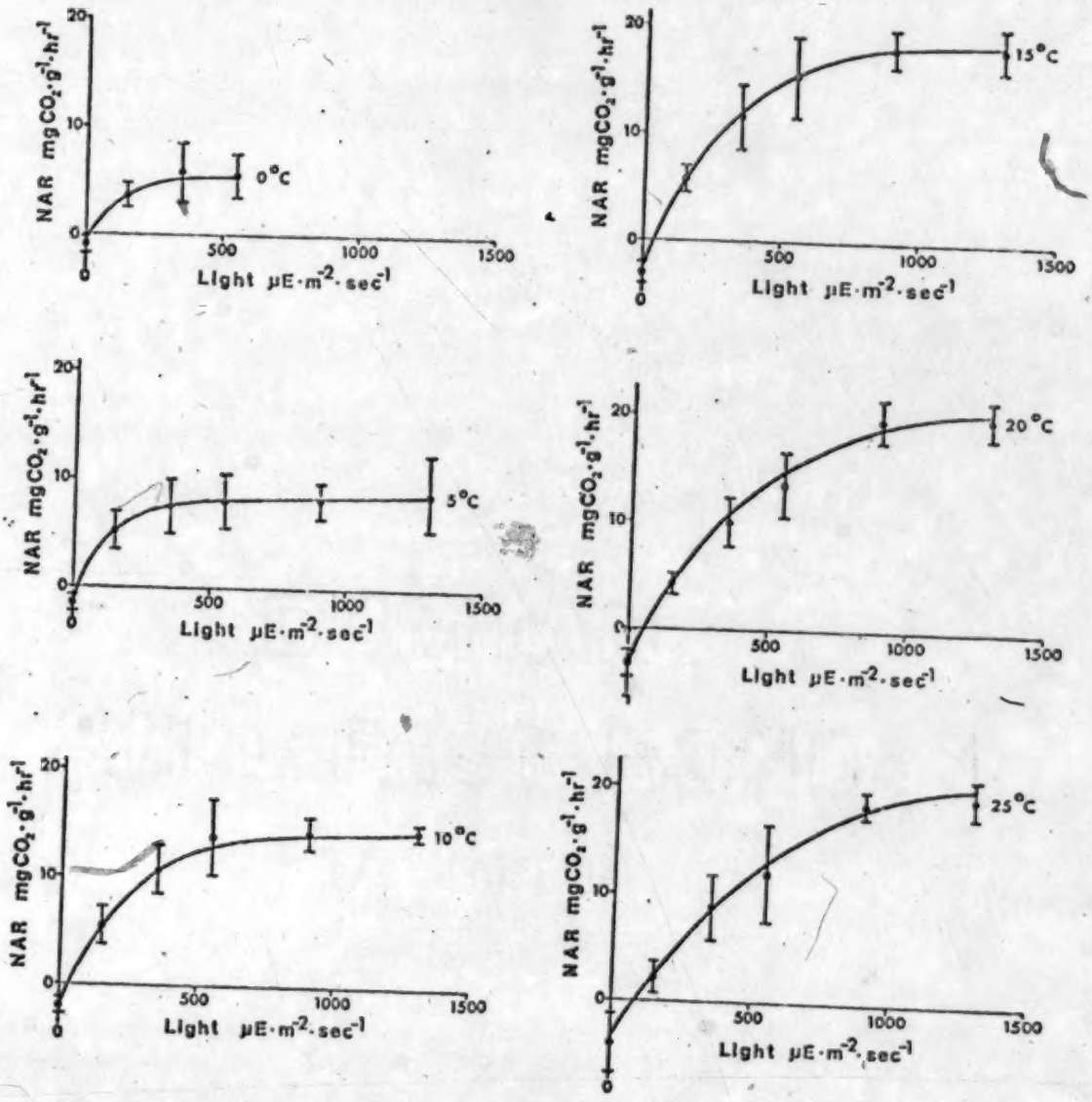

Figure 26. Net photosynthetic light response curves at various temperatures for Luzula confusa. All points area means with 95% confidence limits. Values are of 9-11 tillers from 8 different plants.

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(1600 $\mu E\ m^{-2}\ sec^{-1}$). Both light compensation and ½ light saturation increased with increasing temperature but the rate of increase did not appear to follow the established exponential relationship (Lieth 1960, Pisek 1960). Hartgerink and Mayo (1976) showed that arctic Dryas integrifolia also did not respond exponentially. Luzula confusa had low light compensation and ½ saturation at low temperatures and high light compensation and ½ saturation at high temperatures (Table 20). This appears to be an adaptation of the plant to maintain positive net assimilation in an environment where leaf temperatures are tightly linked to radiation load (see Energy Budgets p 34 ; Addison 1976). This interpretation coincides with Hartgerink (1975) for Dryas from Devon Island, N.W.T. Light compensation and saturation of Luzula confusa at 15°C (180 ft-c and 4800 ft-c respectively) corresponded closely with other arctic graminoids (ca. 125 ft-c and 5000 ft-c; Tieszen 1973).

The use of ½ light saturation rather than saturation in Table 20, stems from the realization that the photosynthetic mechanism is never fully saturated. The data in Fig 26 were fit to Equation 12.

$$NAR = \frac{ax}{b + x} - \text{dark respiration} \quad (12)$$

where a and b are constants and x is light intensity ($\mu E\ m^{-2}\ sec^{-1}$). Half light saturation was determined by calculating maximum NAR, dividing it in half and picking the

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appropriate light level off Fig 26. The use of light saturation however, was maintained for comparison purposes.

Table 20. Light compensation and ½ saturation of Luzula confusa under laboratory conditions. Values are estimates from Fig 26.

TEMPERATURE °C	COMPENSATION µE m^{-2} sec^{-1}	COMPENSATION ft-c*	½ SATURATION µE m^{-2} sec^{-1}	½ SATURATION ft-c*
0	20	120	120	720
5	22	132	110	660
10	25	150	260	1560
15	30	180	350	2100
20	40	240	560	3360
25	60	360	780	4680

* 60 ft-c / µE m^{-2} sec^{-1} (Hartgerink 1975)

Temperature

The optimum temperature of NAR for Luzula confusa (15° to 20°C) agrees well with that exhibited by other arctic plants (Tieszen 1973, Hartgerink 1975, Tieszen and Wieland 1975). Optimum temperature appeared to shift with light intensity (Fig 27). Since light intensity was normally low on King Christian Island owing to high incidence of cloud and fog (see Climatology p 28), under most field conditions the optimum leaf temperature for net photosynthesis would be approximately 15 °C. In the field however, leaf temperatures were normally about 5 to 8 °C and hence there was a strong

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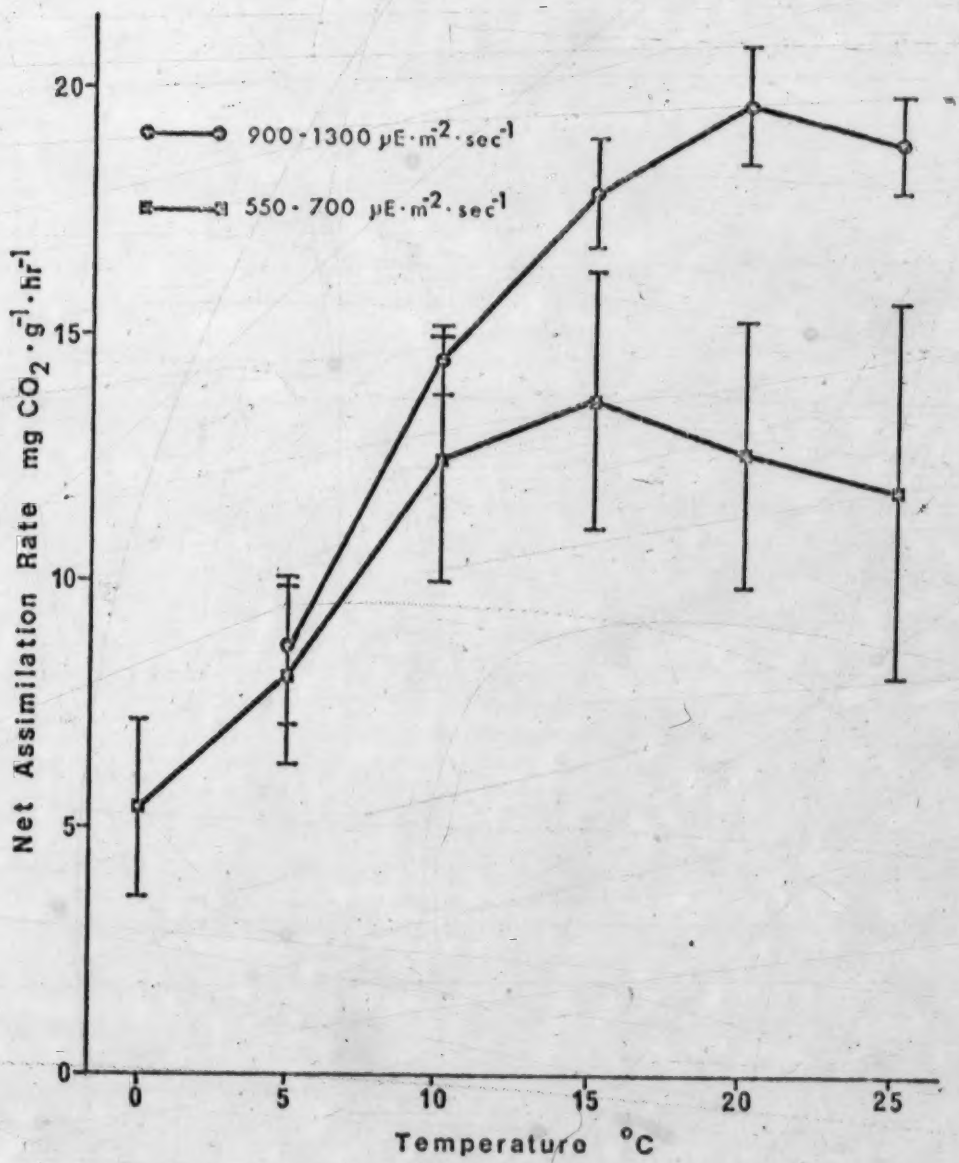

Figure 27. Net assimilation rate of Luzula confusa versus temperature at two different light levels. All points are means with 95% confidence limits.

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dependence of net assimilation on leaf temperature as shown previously (Field Studies p 115). It should be noted that the shift in optimum temperature was a light response and did not represent acclimation of the plant to different thermal and radiation regimes, a process which may also occur (Billings et al. 1971).

Maximum net photosynthetic rate of Luzula confusa (20 mg CO_2 g^{-1} hr^{-1} or 19.3 mg CO_2 dm^{-2} hr^{-1}) was comparable with most other arctic graminoids (10 to 20 mg CO_2 dm^{-2} hr^{-1}; Tieszen 1973). Considering 15 ^{o}C as optimum leaf temperature for net photosynthesis in the field, the maximum net assimilation rate would be about 13.7 mgCO_2 g^{-1} hr^{-1} or 13.2 mg CO_2 dm^{-2} hr^{-1}. This is almost the mid-point of the range of maxima of arctic and alpine graminoids (Tieszen and Wieland 1975).

Dark respiration of Luzula was high at all temperatures (Table 21) and was higher than other arctic graminoids (Tieszen 1973). The rate however, was lower than several other arctic and alpine plants such as Crysothamnus isidiflorus (Mooney et al. 1964), Dryas integrifolia (Hartgerink 1975) and Thalictrum alpinum (Mooney and Johnson 1965). Dark respiration normally increases exponentially with temperature (Larcher 1969) and Luzula (Table 21) appeared to follow this trend. The temperature range chosen for laboratory studies was based on field measurements of leaf temperature and did not go high enough to confirm the exponential

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response. A Q_{10} for dark respiration was 2.1 (5° - 15 °C) and was comparable with both other arctic species (1.8 - 3.0; Semikhatova and Shuktina 1973, Lewis and Callaghan 1974) and other plants in general (2 - 3; Forward 1960).

Table 21. Dark respiration and maximum net photosynthesis of Luzula confusa under laboratory conditions (mean and 95% confidence limits).

TEMPERATURE °C	DARK RESPIRATION mg CO_2 g^{-1} hr^{-1}	MAXIMUM NET PHOTOSYNTHESIS mg CO_2 g^{-1} hr^{-1}
0	0.97 ± 0.75	5.42 ± 2.04
5	1.42 ± 0.77	9.07 ± 3.35
10	1.98 ± 0.77	14.67 ± 0.66
15	2.95 ± 0.89	17.97 ± 2.12
20	3.28 ± 1.36	19.88 ± 1.86
25	3.90 ± 2.71	19.33 ± 1.81

The high rate of respiration of Luzula confusa may be of importance in maintaining high net assimilation rates at low temperatures. High respiration would permit rapid dissolution and translocation of photosynthate and reduce the potential for inhibition of NAR by end-product accumulation (Warren Wilson 1966). Mooney and Billings (1961) suggested that high respiration rates of arctic plants may help them to develop more rapidly in cold environments. Although high

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respiration rate is common to arctic plants, it has yet to be demonstrated why the increased rate is of value to these plants (Billings 1974).

Combined Light and Temperature

The combined effects of light and temperature on net assimilation rate determined in the laboratory aided in the interpretation of field response of Luzula confusa. At low light intensity (ca. 150 $\mu E\ m^{-2}\ sec^{-1}$) and low temperature (ca. 2 ^{o}C), an increase of 0.2 ^{o}C yielded only a 1.4% rise in NAR. A 10% increase in light intensity on the other hand, resulted in an increase of 4.2% in NAR. This indicates that at these low light and temperature levels, NAR was much more sensitive to light changes and hence, the significant correlation of NAR and light shown in the Field Studies (p 115). At higher light intensity, temperature was of greater importance because of the low light saturation of the plant, and the roles of light and temperature were reversed.

Effect of Drying

Water did not appear to be of major significance as a controlling factor for Luzula confusa metabolism on King Christian Island during the 3 year study period (see Water Relations p 102). Both the response of water potential and its components to drying (see Water Relations p 100) and the response of net assimilation rate to drying (Fig 28) indicated

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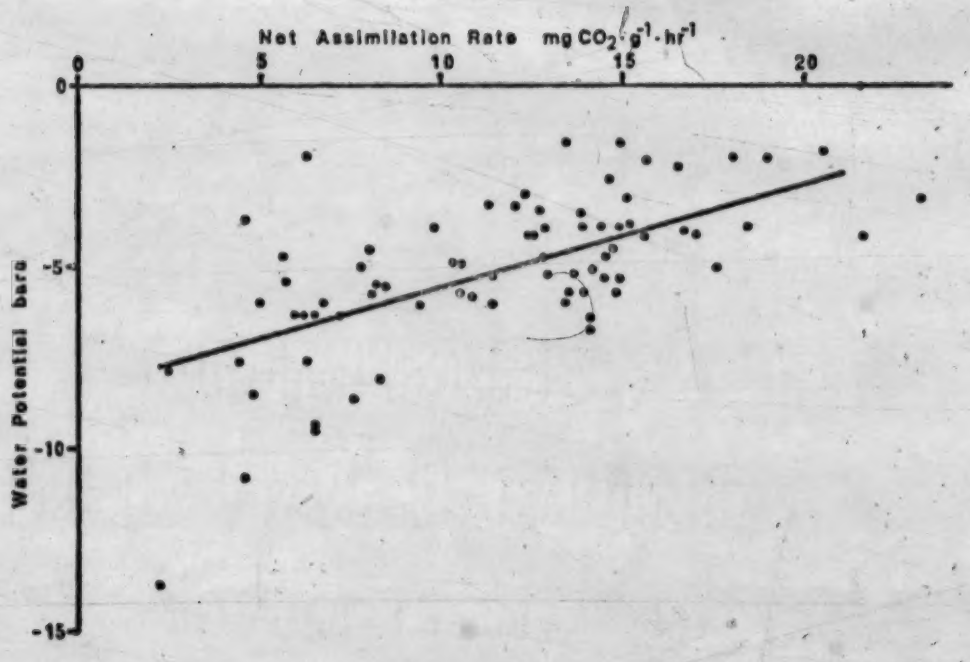

Figure 28. Net assimilation rate of Luzula confusa versus leaf water potential under laboratory conditions. The line was determined through regression analysis.

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that drought stress must indeed be rare since Luzula, which grows over much of the coastal band of King Christian Island, was very intolerant of water deficit. The response of net assimilation to water potential (Fig 28) corresponded to that of alpine plants (Johnson et al. 1974) and increased linearly with increasing water potential (NAR = 29.85 + 3.60 ψ, $p < .001$). Net assimilation rate dropped off dramatically as water potential decreased and was less than 25% of maximum at -7 bars. This reduction was similar to that of Calamagrostis breweri (Klikoff 1965) but much greater than Carex exerta (Klikoff 1965), Dryas integrifolia (Hartgerink and Mayo 1976), Kobresia myosuroides, Geum rossii and Deschampsia caespitosa (Johnson et al. 1974). The latter species however, are native to more xeric environments than is Luzula confusa.

Effect of Phenology

Phenological stage was shown to have a great impact on net assimilation of Luzula confusa. Maximum NAR ranged from 16 mg CO_2 g^{-1} hr^{-1} (540 μE m^{-2} sec^{-1} @ 10 ^{o}C) at anthesis to 5 mg CO_2 g^{-1} hr^{-1} during senescence (Fig 29). The trend in NAR was to increase to a maximum at anthesis and gradually decrease as the plant approached dormancy. The lower values of preflowering NAR (Fig 29) were likely a result of higher respiration rates during growth (Hadley and Bliss 1974, Bliss 1966, Tieszen and Wieland 1974). Reduced postflowering NAR on the other hand, appeared to represent a general slowing

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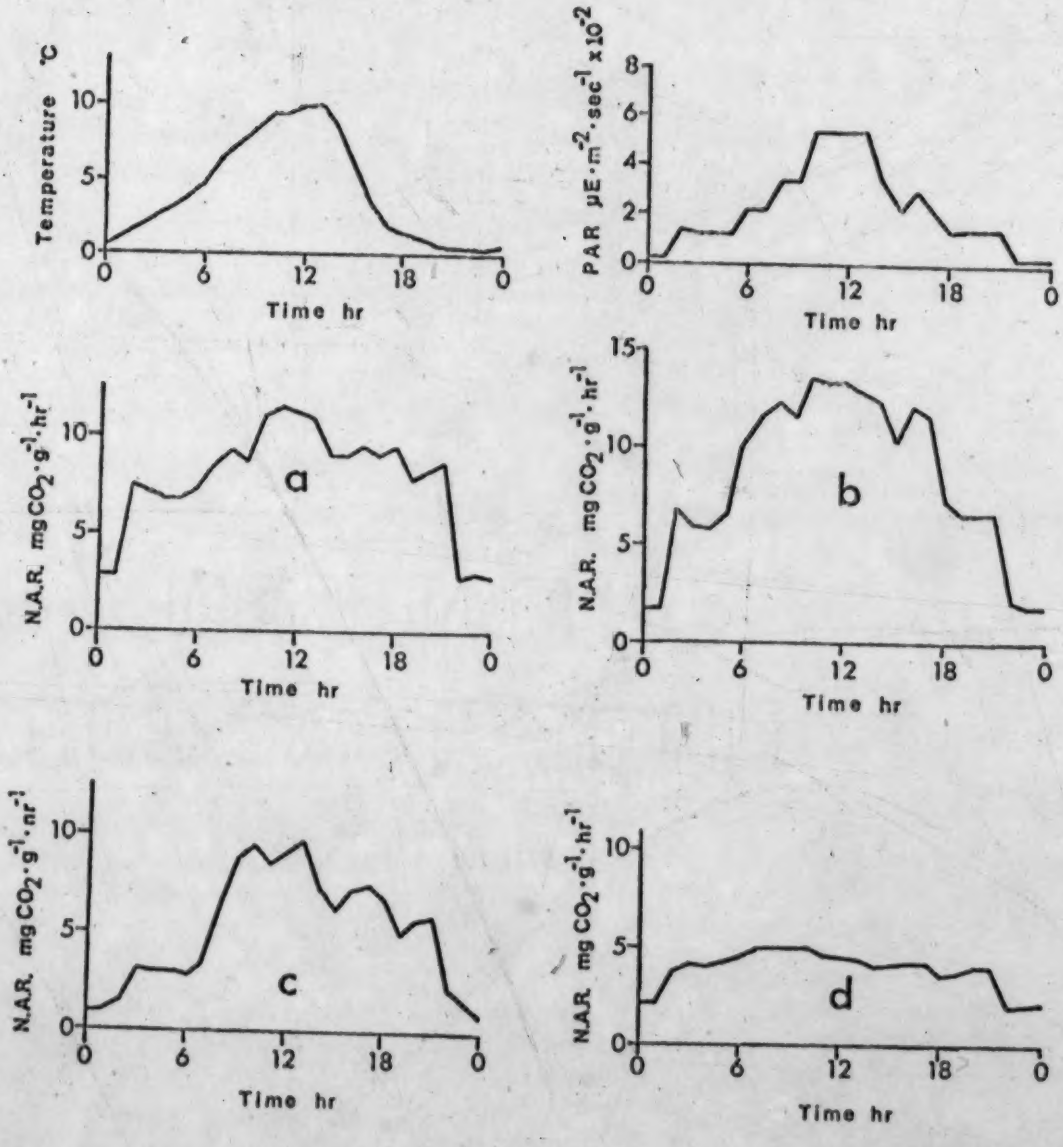

Figure 29. Net assimilation rate of Luzula confusa under four phenological stages in the laboratory; (a) preflowering, (b) anthesis, (c) postflowering and (d) dieback.

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down of plant metabolism with senescence as seen in the field (see Field Studies p 114). This slowing down of both photosynthetic and respiration rates with the onset of dormancy has also been shown for Dryas integrifolia from Devon Island, N.W.T. (Hartgerink 1975). Dryas leaves reached full photosynthetic capacity only at the beginning of the second year of leaf life (Hartgerink 1975) and required a much longer time to mature than did Luzula. The importance of rapid maturation of graminoid leaves (maximum net photosynthetic rate) has been emphasized by the simulation studies of Miller and Tieszen (1972) which showed a doubling of annual biomass production if leaf area was doubled in the spring.

Simulation Studies

An empirical model was developed to try to estimate net photosynthetic rate and annual biomass production of Luzula confusa in the field. Leaf temperature, light intensity (PAR) and water potential were used as input parameters since measurements were available for an entire growing season (July and August, 1973). The structure of the model was based on relationships between net assimilation rate and light, temperature and water potential that had been established under laboratory conditions.

A log -log plot of NAR versus light intensity was linear at all temperatures (0 - 25 ^{o}C) and was described by

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Equation 13.

$$\text{Log}_{10}(\text{NAR}+5) = a + b(\text{Log}_{10}(L + 1)) \qquad (13)$$

where a and b are variables based on temperature and L, light intensity ($\mu E\ m^{-2}\ sec^{-1}$, PAR). The responses of a and b to temperature were also found to be linear and Equations 14 and 15 were derived.

$$a = 0.721 - 0.027(T) \qquad (14)$$

$$b = 0.1516 + 0.0118(T) \qquad (15)$$

where T is leaf temperature (^{o}C). Regression analysis was used to determine the constants for all curves and the linear regressions described above were all significant ($p < 0.01$; Sokal and Rohlf 1969, p. 420).

The linear regression of NAR on water potential described previously (see Effect of Drying p 126) was used to simulate the influence of moisture on NAR. The model used a threshold of -2 bars however, and NAR was calculated for -2 bars and the actual water potential. The percentage of maximum NAR was then calculated and multiplied by the value of NAR determined in Equation 13.

Under laboratory conditions, the model predicted values of net assimilation that fell between measured values of NAR for preflowering and postflowering phenological stages (Fig 30). Much of the difference between

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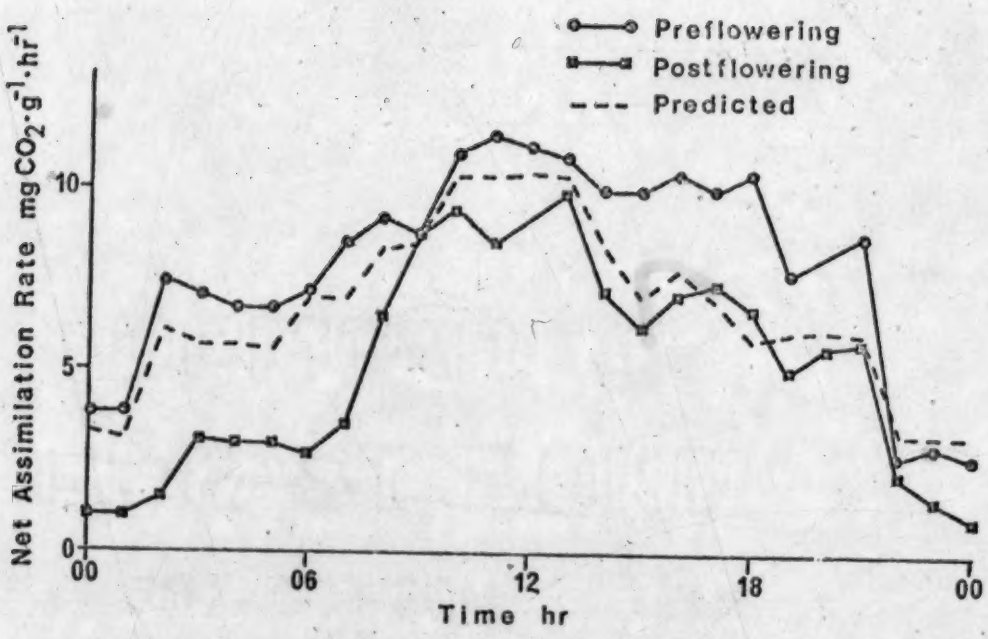

Figure 30. Comparison of predicted versus measured values of net assimilation rate under laboratory conditions.

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predicted and measured values can be accounted for by the variability among individual plants and the fact that phenology was not taken into consideration when the response of net photosynthesis to light, temperature and water were determined. The model therefore, appeared to be capable of estimating NAR of an "average" Luzula plant in the laboratory.

In the field, the model based on laboratory responses was not as effective as in the laboratory and the difference between measured and predicted net photosynthetic rates were substantial (Fig 31). The model overestimated NAR at low light and temperature, and underestimated NAR at high light and temperature. The reason for descrepancies between predicted and measured values is not known but, it is thought that the laboratory plants may have acclimated to the lower light intensities under which they were grown in the environmental growth chambers (see Water Relations p 83). This might account for the higher NAR at low light and lower NAR at higher light as compared with field plants. The ability of arctic and alpine plants to acclimate to growing conditions is well known (Mooney and West 1964, Billings et al. 1971). The lower than predicted NAR of field plants may also be a result of cold soil temperatures. Low soil temperature has been shown to severely reduce plant growth in beans (Brouwer 1964) and corn (Kleinendorst and Brouwer 1970) as well as in arctic and alpine plants (Bliss 1966, Bell 1975). The empirical nature of the model made it almost impossible to use

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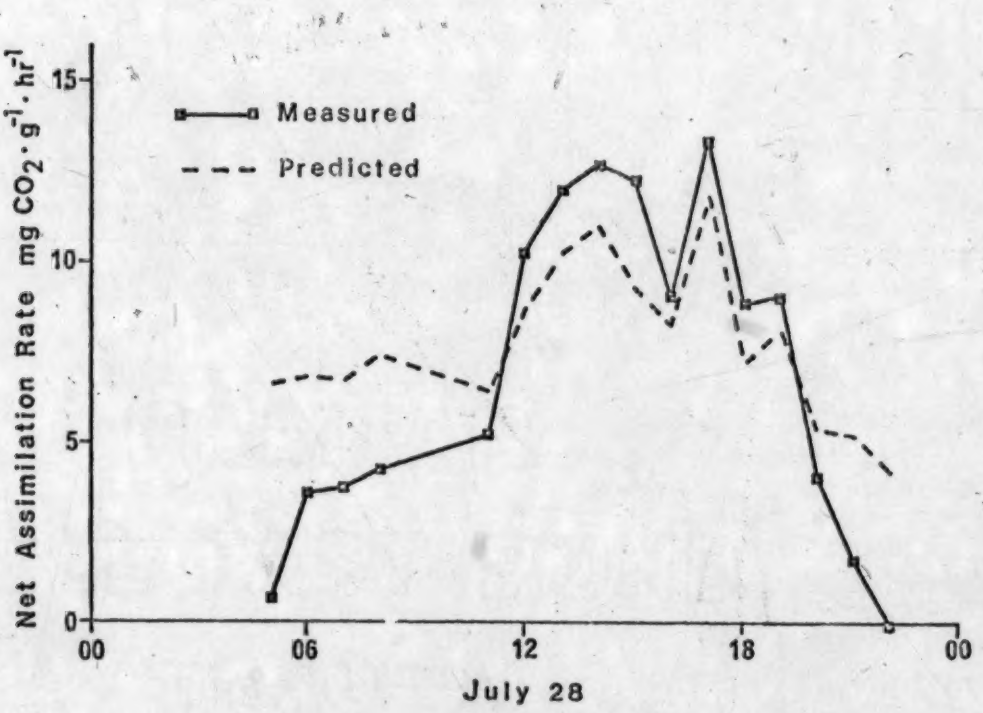

Figure 31. Comparison of net assimilation rate predicted using the laboratory model and field conditions and that measured under field conditions.

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it except under the narrow range of plant and environmental conditions under which it was derived. This was illustrated by the poor predictive capabilities of the laboratory model under field conditions.

The model of net assimilation based on single factor analysis and derived from field data, appeared to be fairly accurate (see Field Studies p 117) and was used to predict the photosynthetic capabilities of Luzula confusa in the King Christian Island Environment. Although it was not possible to calculate production of Luzula because live standing crop was not measured throughout the season, Fig 32 shows that the potential for net photosynthesis was much higher in the spring and early summer than in the late summer and fall. This illustrates the importance of immediate initiation of growth in the spring that is characteristic of Luzula. The model of Miller and Tieszen (1972) also showed that early spring initiation of growth would dramatically increase the productivity of Dupontia fischeri in the wet coastal meadows at Barrow, Alaska.

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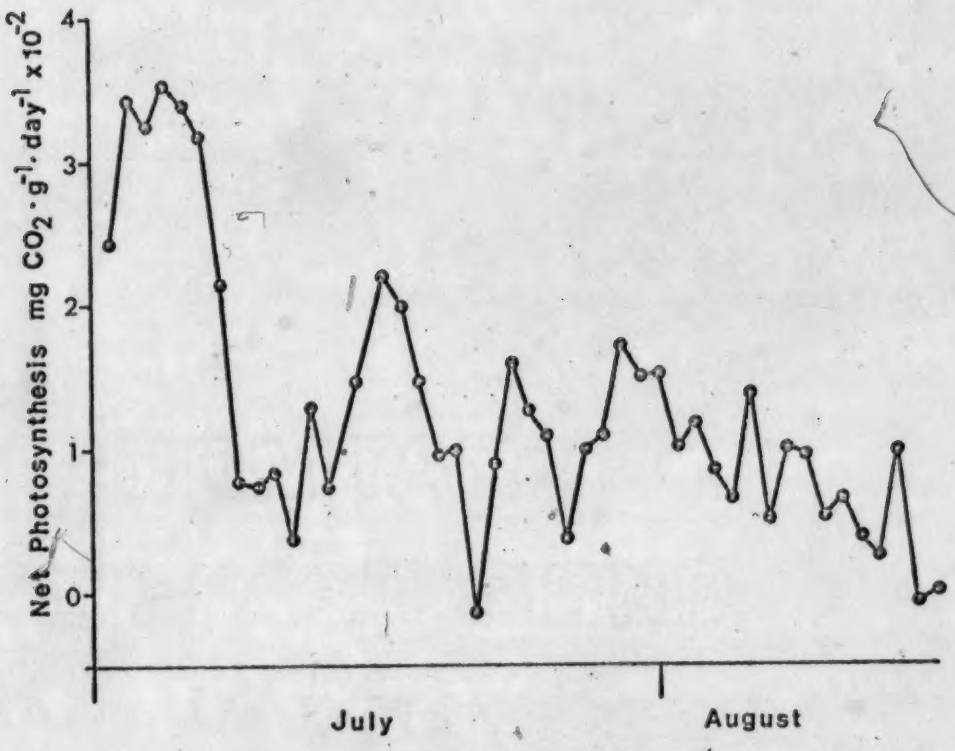

Figure 32. Potential net photosynthetic rate (field model) based on actual field conditions during the summer of 1973.

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ECOLOGICAL IMPLICATIONS

King Christian Island is a small island (ca. 1000 Km^2) in the Sverdrup Group, but its importance to man far exceeds its relative size. The reason for this lies below the island and surrounding ocean in its reserves of natural gas. One of the first discoveries of natural gas in the Arctic Islands was on King Christian Island and hence, man has been an important component of this ecosystem for several years. The involvement of man in this ecosystem is characterized by his disturbance of the natural system through solid and liquid waste disposal, surface blading, seismic and drilling operations, vehicle tracks, and airstrip construction and maintenance (Babb and Bliss 1974, Addison and Bell 1976). Although all of these disturbances are local in nature, revegetation must be considered both because of government regulations, the need of industry to maintain intact and stable land surfaces and for aesthetic reasons.

Wind and water erosion appear to be very important factors in the establishment of the highly dissected surface features on King Christian Island. The more complex topography thus formed, gives rise to gradients in exposure, available soil water and soil stability and hence, a variety of different microenvironments. Plant communities in the Polar Semi-desert appear to be delimited by these microenvironments whereas in the Polar Desert, no definite plant communities could be discerned owing to the sparse vascular

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plant cover (< 1%). The Polar Semi-desert area (2 - 15% vascular plant cover) occurs in a band about 1.5 Km wide, 1 Km from the coast. The rest of the island is Polar Desert (< 2% vascular plant cover).

The climate of Cape Abernathy, King Christian Island in summer can be classified as maritime, regardless of whether ice leaves the ocean to the north (Danish Strait) or not. In 1973, ice left Danish Strait on July 17 and originally, it was felt that this was responsible for the high incidence of fog. In 1974 however, ice did not leave but fog frequency was still high, It seems therefore, that the influence of wet land surfaces has been underestimated and that much of the moisture contributing to local fog banks was from this source. The greater precipitation in 1973 than in 1974 (47 vs 39 mm) is thought to have resulted from greater cyclonic activity with a more northerly position of the arctic front. The greater frequency in cyclonic activity was also reflected in cloud cover (85% in 1973 vs 77% in 1974).

Summer climate of the area, based on two years of observations (1973-74), was characterized by low temperatures (2.5°C), low precipitation (43 mm), moderate wind speeds (3.3 m sec^{-1}), high relative humidity (90 - 95%) and a high incidence of cloud and fog (80%). These values compare closely with the summer climate (July and August) at Isachsen, Ellef Ringnes Island; the closest permanent meteorological site.

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Thermal regime appears to dominate the King Christian Island environment. Since air can hold only very little water vapour at low temperatures and surface to air temperature gradient was shallow, evapotranspiration was at a minimum. Cloud cover however, was high and this completed the cycle by reducing the amount of global radiation received and keeping both thermal gradient (surface to atmosphere) and air temperature low.

Longwave radiation fluxes were the major components of the surface radiation balance and, because of their magnitude, net radiation appeared to be an exceptionally large component of global radiation (68%) by temperate standards. In general, net radiation was quite comparable with other arctic sites. Latent heat flux was low apparently as a result of a very shallow surface to atmosphere water vapour gradient. Resistances to both mass and convective heat transfer were small because of both the wind speed and the meteorologically smooth surface. Energy dissipation appeared to be controlled mainly by physical rather than physiological factors since vascular plants, non-vascular plants and bare soil all responded to the radiant heat load in a similar manner.

Wind appears to be a major factor that delimits the distribution of plants on King Christian Island. Not only is it important from an energy and mass transfer point of view as mentioned above, but it may also be responsible

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for mechanical damage to plants. The impact of wind depends on speed, surface roughness and particulate load. The results of abrasion by wind-borne sand and ice particles were observed more often in Polar Desert than in Polar Semi-desert areas. These features included polishing of exposed stones, small blow-outs around plants and rocks, deposition of material over plants and, abrasion of plant parts exposed during winter. Both the expansion and contraction of the soils with changing soil moisture and manual texturing, indicated that in general, Polar Semi-desert areas had higher silt and clay contents than Polar Desert areas. The greater incidence of wind erosion features in Polar Desert than in Polar Semi-desert areas appears to be related to surface stability as a result of parent material.

The growth form of Luzula confusa appears to be one of the dominant plant characteristics that accounts for its success in the high arctic environment. Both aboveground and belowground parts of Luzula are concentrated near the soil-atmosphere interface. Since the source of heat for both atmosphere and soil is the earth's surface, the growth form of L. confusa appears to be ideally suited to utilize the warmest thermal environment available on King Christian Island. Persistance of dead material in its upright position is also important in ameliorating the thermal regime. Standing dead material helps to decrease the influence of wind on heat flux and results in leaf temperatures being warmer than air temperature. Standing dead material

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remains intact for a long period of time (>20 years) because its upright position puts the substrate in a hostile environment for decomposition and grazing by animals is negligible. Visser (pers. comm.) found that both fungal biomass and number of fungal species colonizing dead Luzula confusa leaves were extremely low compared with fungal populations on leaves in more temperate regions. The large amount of standing dead (94% of aboveground standing crop) appears to aid in protection of living plant parts. In winter, snow accumulates around the dead material protecting the basal meristem from both abrasion by wind-borne ice particles and extremes of temperature. In spring, trapped snow melts and provides additional water to the plant for the growing season.

A moss layer (0 - 2 cm) was usually associated with Luzula confusa and it appears to be partially responsible for plant survival and growth in several respects. A moss mat provides protection for the plant's meristem throughout the year and acts as a water reservoir. Water may be limiting to plant growth, either on exceptionally dry years (which appear to be rare), or each year while the mineral soil is frozen or very cold. The utilization of the moss layer as a rooting medium (6% of Luzula root biomass) may be necessary for rapid initiation of growth in spring since water needed for elongation would not be available from frozen mineral soil. The most important roll of the moss mat however, appears to be as a seedbed.

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Addison and Bell (1976) showed that germination and subsequent establishment of native species on King Christian Island was greatest on a moss substrate. It appears that Luzula confusa utilizes this substrate as a seedbed which may be not only beneficial but essential for plant establishment.

Reproduction of Luzula confusa is mainly asexual through production of new tillers from underground rhizomes every 3 - 4 years. Each tiller lives for about 7 years and dies after flowering in its final year. Flowering appears to stimulate rhizome branching, possibly through the loss of apical dominance as a result of the shift from leaf to floral meristem. Each rhizome branch supports two living tillers and hence, rhizome branching increases asexual reproduction substantially. Since no viable Luzula seed was found during the three year study period, even flowering appears to be more important for asexual than sexual reproduction.

Water did not appear to be a limiting factor for survival and growth of Luzula confusa on King Christian Island. The major reason for this appears to be consistently high ambient relative humidity and shallow surface to atmosphere temperature gradient both of which kept evapotranspiration low. During the three years of study, evaporation to precipitation ratio was low enough that

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near surface soil moisture (0 - 5 cm) did not drop below -5 bars during any growing season. In spite of high soil moisture, Luzula did experience leaf water deficit on rare occasions, owing to the effects of low soil temperatures and a steep leaf to atmosphere moisture gradient. At these times, turgor potential approached zero and leaf resistance to water flux increased dramatically indicating stomatal closure. Since water vapour and carbon dioxide fluxes have similar pathways, stomatal closure would decrease both transpiration and photosynthesis to almost zero. Under controlled conditions in the laboratory, net photosynthesis dropped dramatically with decreasing leaf water potential (< 25% of maximum at - 7 bars). The physiology of Luzula therefore, appears to be suited to non-drought conditions and even slight water deficit may substantially influence plant carbon balance that is critical at these latitudes. The periodicity of Luzula confusa may have evolved as an avoidance of late season droughts rather than as a protective mechanism to prevent winter injury as suggested by Savile (1972).

Low summer temperature appears to be the dominant environmental factor responsible for low growth rates of plants in arctic environments (Tieszen 1972, Billings 1974). In spite of the growth form of Luzula which tends to ameliorate the thermal regime, temperature still appears to be the factor that is most influential. Both above and belowground temperatures are important in plant functioning

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but growth and development of arctic and alpine plants are affected more by soil than air temperatures (Bliss 1966, Dennis and Johnson 1970). This is probably caused by the combined effects of low decomposition rates resulting in slow nutrient cycling, and low root activity in uptake of nutrients and water (Douglas and Tedrow 1959, McCown 1975). Soil temperatures in the rooting zone of Luzula (-5 cm) on King Christian Island were low, averaging 3.1°C during the growing season (July and August, 1973). Both plant communities had similar soil temperatures at this depth and at no time did the daily mean soil temperature exceed 10°C. Over 80% of Luzula confusa roots were in the surface 5 cm of soil and this morphological adaptation to utilize the warmest soil environment is probably extremely important in the success of the species. More detailed considerations of root growth and adaptations on King Christian Island are found in Bell (1975).

Leaf temperature of Luzula was 1 to 2 ° above ambient air temperature (2.5°C) during the 1973 growing season on King Christian Island. Although this difference was small as compared with several other arctic plants at other arctic sites (Warren Wilson 1957, Corbet 1972, Addison 1976), it appeared to have a substantial influence on net photosynthesis. The field model of net photosynthesis estimated a 250% increase in net assimilation rate with a 1 C° rise in temperature at 3°C (1.0 vs 3.5 mg CO_2 g^{-1} hr^{-1}). In general,

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both photosynthesis and dark respiration operated at low temperatures, and positive net photosynthesis was observed at -2 to -3°C both in the field and laboratory. Air temperature rarely drops below 0°C during the 50 day growing season. Both the ocean and the large volume of water in the soil ameliorate the thermal regime and hence, Luzula confusa is not exposed to very low temperatures while in an active state. The adaptive significance of fairly high dark respiration rates at low temperatures appears to be related to the need to develop rapidly in a short and cool growing season (Mooney and Billings 1961, Billings 1974).

The response of net photosynthesis of Luzula to light intensity was similar to the general response of a C_3 plant. Light compensation was comparable with other arctic plants and permitted the plant positive net assimilation rates even under low illumination. Luzula showed a similar strong coupling of net photosynthesis to radiation intensity as reported by Shvetsova and Voznessenskii (1971) and Tieszen (1973) but, the response was probably an indirect effect of light through radiant heating of leaves. In the field, light intensity rarely appeared to be limiting to net photosynthesis. Light quality appeared very consistent and no shift in red to far red ratio was detected either seasonally or on a diurnal basis. It does not appear therefore,

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that the 660/730 Phytochrome response is involved in the biological timing of Luzula confusa. The periodicity of Luzula did not require an external stimulus since flowering, fruiting and dieback all occurred in a controlled environment chamber under a constant day-night pattern of environmental conditions.

Prediction of Luzula net assimilation rate based on environmental conditions indicated the importance of rapid spring initiation of growth. Since the short arctic growing season is one environmental factor that plants cannot control, maximum utilization of season may be important in maintaining a positive carbon balance. Luzula confusa initiated growth within one day of snow-melt and since time of melt was usually in late June or early July, it took advantage of the optimum conditions availabe for net photosynthesis (see Fig 32). Rapid production of green material was made possible by pre-formed buds and partially extended green leaves that persisted over winter. Spring growth appeared to be at the expense of carbohydrate reserves stored in both stems and rhizomes.

Based on the physiological characteristics of Luzula confusa, the most important feature that a plant selected for revegetation must have, is the ability to assimilate carbon positively and rapidly at low temperatures. This ability may be achieved by either physical characteristics

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ameliorating the thermal regime of physiological characteristics that permit rapid carbon assimilation at low temperatures. In addition, plants that utilize the early part of the growing season have a greater likelihood of survival, growth and reproduction in this high arctic environment.

In general, Luzula confusa appears to be both morphologically and physiologically adapted to the Polar Semi-desert environment on King Christian Island. This species combines the more efficient graminoid photosynthetic system with some of the cushion plant energy trapping characteristics. In this way, the plant is able to assimilate carbon throughout the arctic 24 h day as well as positively and rapidly at low temperatures. In addition, the plant takes advantage of the optimal growing conditions that occur immediately after snow-melt.

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Appendix A. Light quality of growth chamber lamps at various times during an artificial day. Values are in $\mu W\ m^{-2}\ nm^{-1}$ from a spectralradiometer at 90 cm.

Wavelength nm	Light Intensity at 0000	0600 & 1800	1200
400	0.80	3.12	4.40
425	1.54	5.40	8.51
450	3.16	10.75	14.28
475	2.58	7.75	10.54
500	2.78	8.20	11.00
525	3.06	9.44	12.65
550	7.84	29.57	35.95
575	8.51	27.81	35.64
600	8.32	25.33	33.71
625	5.32	15.68	20.78
650	3.01	8.47	10.81
675	1.84	4.59	5.66
700	1.27	2.70	3.23
725	1.06	1.90	2.19
750	1.02	1.73	1.87
800	1.20	2.22	2.18
850	1.22	2.07	2.17
900	1.19	1.44	1.56
950	1.30	1.59	1.65
1000	1.69	2.88	3.39
1050	1.63	2.92	3.65
1100	1.28	1.42	1.46
1150	1.29	2.01	2.26
1200	0.88	0.98	1.06
1250	0.95	1.06	1.11
1300	0.85	0.95	0.99
1350	0.66	0.94	1.00
1400	0.54	0.89	1.03
1450	0.43	0.49	0.52
1500	0.44	0.58	0.61
1550	0.42	0.72	0.81

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Appendix B

One of the most difficult factors to quantify in ecophysiological studies is the level of confidence that can be placed in any measurement of environmental factors. Since it was not possible to replicate radiation regime, water relations and several temperature measurements, some idea of accuracy was necessary before interpretation of the results was possible. There are two types of errors involved; 1) those owing to the instrument, its calibration and the recorder, and 2) those owing to positioning of the sensor. No estimate of this latter error was possible and the following table outlines the potential errors owing to instrumentation. In the table, only systematic errors were considered and random errors have been omitted since most measurements were long-term averages.

UNCERTAINTY SOURCE	SYMBOL	VALUE
Thermocouple	T_c	.2°C
Electronic reference	Er	.5°C
Recorder	B	.5% of full scale
Thermistor recorder	Tr	1°C
Albedometer	A	1%
Net Radiometer	F	2.5%
Black Body Emissivity	ε^o	.05
Surface Emissivity	ε	.05
Quantum Sensor	Q	2%
Weight	W	.1 g
Heat Flux Plate	P	5%
Vapour Pressure Leaf	$VP(T_1)$	.28 mm Hg
Vapour Pressure Air	$VP(T_a)$	.39 mm Hg
Thermocouple	T_{c1}	.1°C
Meter	D	2.5% of full scale
Fresh-Dry Weight	W_1	1 mg
Turgid-Dry Weight	W_2	1 mg

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Appendix B (continued)

CONSTANTS	VALUE
K_1	2.13 °C/mv
K_2	.14 cal cm^{-2} min^{-1}/mv
K_3	.04 cal cm^{-2} min^{-1}/mv
K_4	241.5 μE m^{-2} sec^{-1}/mv
K_5	.093 cal cm^{-2} min^{-1}/mv
K_6	.06 cal cm^{-2} min^{-1}/mv
K_7	2. bars/μv

FACTOR	SOURCE OF ERROR	EQUATION	UNCERTAINTY
Leaf Temperature (T_l)	Thermocouple, Electronic reference, Recorder	$\delta T_c + \delta Er + K_1 \delta B$	.71°C
Air and Soil Temperature	Thermistor recorder	δTr	.1°C
Air Temperature (T_a)	Hygrothermograph		1°C
Relative Humidity (RH)	Hygrothermograph		5%
Wind Speed	a. Totalizing Anemometer b. Hot Wire Anemometer		5% 2%
ENERGY			cal cm^{-2} min^{-1}
Global (R_T)	Albedometer, Recorder	$K_2(\delta A + \delta B)$	.008
Reflected (R)	Albedometer, Recorder	$K_2(\delta A + \delta B)$	.008
Incoming (I)	Net Radiometer, Recorder, Temperature, Black body emissivity	$K_3(\delta F + \delta B) + \sigma T_l^4(\frac{\delta \epsilon^o}{\epsilon} + 4\frac{\delta T_l}{T_l})$	.048
Longwave Down	Incoming, Global	$\delta I + \delta R_T$	.056
Longwave Up (L_u)	Temperature, Surface emissivity	$\sigma T_l^4(\frac{\delta \epsilon}{\epsilon} + 4\frac{\delta T_l}{T_l})$	.027
Net (R_n)	Incoming, Reflected, Longwave Up	$\delta I + \delta R + \delta L_u$	.083
Latent Heat (LE)	Weight	$K_5(\delta W)$	.009
Soil Heat (G)	Heat Flux Plates, Recorder	$K_6(\delta P + \delta E)$	.006
Sensible Heat	Net Radiation, Latent Heat, Soil Heat	$\delta R_n + \delta LE + \delta G$	.098
Photosynthetically Active Radiation	Quantum Sensor, Recorder	$K_4(\delta Q + \delta B)$	16.9 μE m^{-2} sec^{-1}
Vapour Pressure Gradient (VP)	Temperatures, Relative Humidity	$\delta VP(T_l) + RH \cdot VP_a(\delta VP(T_a) + \delta RH)$	.91 mm Hg
Resistance to Water Flux	Temperature, Vapour Pressure, Water Loss	$\frac{273}{760T_l}\frac{\rho VP}{E}(\frac{\delta T_l}{T_l} + \frac{\delta VP}{VP} + \frac{\delta E}{E})$	1.41 sec cm^{-1}
Air Resistance	Temperatures, Sensible Heat	$1.82c\rho(\frac{T_l - T_a}{H}) \cdot$	
		$(\frac{\delta T_l}{T_l} + \frac{\delta T_a}{T_a} + \frac{\delta H}{H})$	.45 sec cm^{-1}
Leaf Water Potential	Thermocouple, Meter	$K_7(\delta T_{cl} + \delta D)$	.7 bars
Osmotic + Matric Potential	Thermocouple, Meter	$K_7(\delta T_{cl} + \delta D)$	.7 bars
Turgor Potential	Thermocouples	$K_7(2\delta T_{cl})$	.4 bars
Relative Water Content	Weight	$100(\frac{\delta W_1}{W_1} + \frac{\delta W_2}{W_2})$	2.2%
Coefficient of Expansion	Osmotic + Matric, Turgor Potentials, Relative Water Content	$(\Psi_{om} - \frac{\Psi_{om} - \Psi_p}{1 - RWC}) \cdot$	
		$(2\frac{\delta \Psi_{om}}{\Psi_{om}} + \frac{\delta \Psi_p}{\Psi_p} + \frac{\delta RWC}{RWC})$	0.7 bars ΔRWC